Mathematical Modeling and Mathematical Analysis in Mathematical Biology

July 1-July 10,2019

1 Lecture 1 Simple Chemostat Equation

Outlines: Derivation of simple chemostat equations; Competitive exclusion principle in simple chemostat equations; McGhee's proof for general monotone functional responses; Hsu's Lyapunov function; Wolkowicz and Lu's Lyapunov function for type III; Fluctuating lemma and its applications to simple chemostat equation with delays.

Derivation of simple chemostat equations:

From Monod's experiments (1942), we have the following basic assumptions:

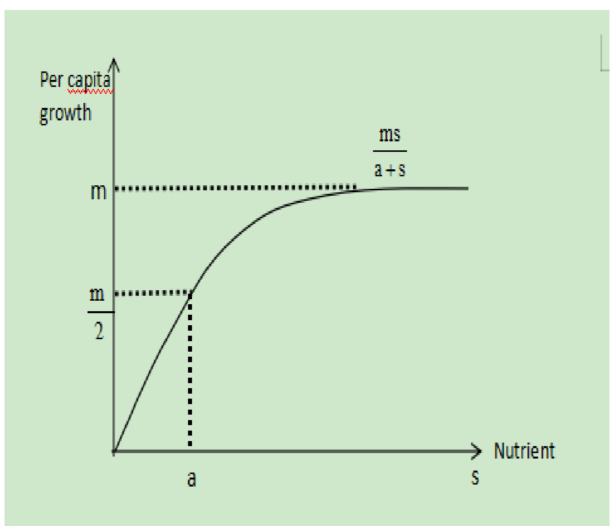

Figure 1:

By Fig. 1, m is the maximal growth rate; a is the half-saturation constant.
(ii)

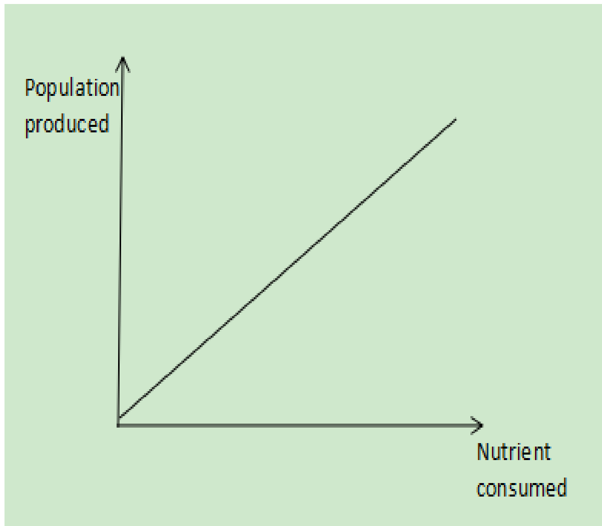

Figure 2:

Let

$S(t)$ = concentration of nutrient at time t. $(mass/vol)$
$x_i(t)$ = concentration of i-th micro-organBM at time $t, i = 1, 2, ..., n$ $(mass/vol)$
$S^{(0)}$ = Input concentration of nutrient (mass/vol)
f = flow rate (vol/time)
V = Volume of Chemostat
D = dilution rate = $\dfrac{f}{V}$ (1/time)
γ_i = yield constant = $\dfrac{\text{nutrient consumed}}{\text{population produced}}$ $(by\ Fig.\ 2)$
m_i = max growth rate for i-th species
a_i = half-saturation for i-th species

Based on the Principle of modeling:

Rate of Change=Input-Output

we have:

$$\begin{aligned} V\frac{dS}{dt} &= \text{Rate of change of nutrient in the chemostat} \\ &= f\cdot S^{(0)} - f\cdot S(t) - \sum_{i=1}^{n}\frac{1}{\gamma_i}\frac{m_i S}{a_i+S}x_i V \\ V\frac{dx_i}{dt} &= \text{rate of change of i-th species} \\ &= \frac{m_i S}{a_i+S}x_i V - f\cdot x_i(t) \end{aligned}$$

we obtain simple chemostat equation

$$\begin{cases} \dfrac{dS}{dt} = (S^{(0)}-S)D - \sum\limits_{i=1}^{n}\dfrac{1}{\gamma_i}f_i(S)x_i, \\ \dfrac{dx_i}{dt} = (f_i(S)-D)x_i, \\ S(0)\geq 0 \quad x_i(0)>0, \quad i=1,2,...,n \end{cases}$$

Theorem 1.1. [HHW1] *Let* $m_i > D$, $\frac{m_i\lambda_i}{a_i+\lambda_i} = D$ *or* $\lambda_i = \frac{a_i}{(\frac{m_i}{D})-1}$ = *break-even concentration of i-th species. If* $0<\lambda_1<\lambda_2<...<\lambda_n$, $\lambda_1 < S^{(0)}$, *then the competitive exclusion principle holds, i.e.* $\lim\limits_{t\to\infty} S(t) = \lambda_1, \lim\limits_{t\to\infty} x_1(t) = x_1^* = S^{(0)} - \lambda_1$, $\lim\limits_{t\to\infty} x_i(t) = 0$, $i = 2, ..., n$.

Biological interpretation: The species with smallest break-even concentration wins the competition. Let $r_i = m_i - D_i$ =intrinstic grow rate, then λ_i can be rewritten as $\lambda_i = \frac{a_i D}{r_i}$. If $r_1 = r_2 = ... = r_n$, then the one with smallest half-constant wins the competition.

McGhee's generalizations[AM] [SW]:

Cosider

$$(1)\begin{cases} \dfrac{dS}{dt} = (S^{(0)}-S)D - \sum\limits_{i=1}^{n}\dfrac{1}{\gamma_i}f_i(S)x_i, \\ \dfrac{dx_i}{dt} = (f_i(S)-D)x_i, \\ S(0)\geq 0 \quad x_i(0)>0, \quad i=1,2,...,n \end{cases}$$

$f_i(S)$ satisfies

(i) $f_i(0) = 0$

(ii) $f_i'(S) > 0$

Example:

(i) $f_i(S) = k_i S$ Type I

(ii) $f_i(S) = \frac{m_i S}{a_i+S}$ Type II

(iii) $f_i(S) = \frac{m_i S^n}{a_i+S^n}$ Type III

Theorem 1.2. *Let λ_i satisfies $f_i(\lambda i) = D$. if $0 < \lambda_1 < \lambda_2 < ... < \lambda_n$, $\lambda_1 < S^{(0)}$ then competitive exclusion principle holds.*

Proof. Step 1: Conservation principle: For simplicity, we assume $\gamma_i = 1$ $i = 1, ..., n$. Then

$$S' + x_1' + ... + x_n' = S^{(0)}D - (S + x_1 + ... + x_n)D$$

$$S(t) + x_1(t) + ... + x_n(t) = S^{(0)} + O(e^{-Dt})$$

Consider limiting equation

$$(2) \quad \frac{dx_i}{dt} = (f_i(S^{(0)} - \sum_{i=1}^{n} x_i(t)) - D)x_i, \ i = 1, 2, ..., n$$

From [SW](Appendix F, A Convergence Theorem), system (1) and system (2) have the same solution behavior.

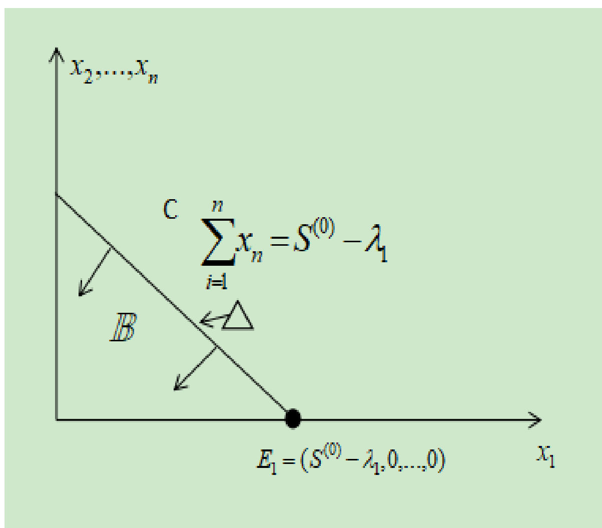

Figure 3:

By Fig. 3

$$\triangle = \{(x_1, ..., x_n) : \sum x_i = S^{(0)} - \lambda_1\}.$$

$$C = \{(x_1, ..., x_n) : \sum x_i > S^{(0)} - \lambda_1\}.$$

$$\mathfrak{B} = \{(x_1, ..., x_n) : \sum x_i < S^{(0)} - \lambda_1\}.$$

we can check that if the trajectory enter the region $\mathfrak{B}$, then it stay there.(See Fig. 3)

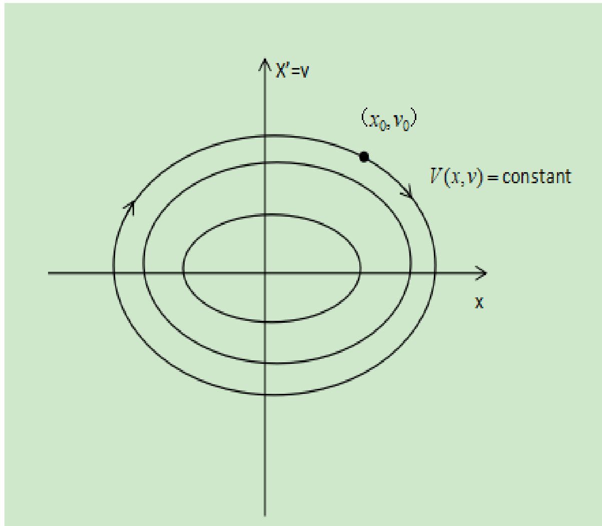

Figure 4:

Case 1. if the trajectory stays in C, then it converges to E_1 by using Lyapunov functions. $V(x_1, ..., x_n) = \sum_{j=1}^{n} x_j$.

Case 2. if the trajectory stays in $\mathfrak{B}$ the trajectory converges to E_1 by using Lyapunov functions. $V(x_1, ..., x_n) = -x_1$.

□

Lyapunov functions[H]

Example 1: Simple harmonic motion

$$mx'' + kx = 0, \qquad x' = v.$$

Let

$$V(x, v) = \frac{mv^2}{2} + \frac{kv^2}{2} = \text{kinetic energy+potential}.$$

Then $\frac{d}{dt}V(x, v) \equiv 0$. i.e. energy conserved.

Example 2:

$$\begin{cases} x'' + g(x) = 0, \\ xg(x) > 0, \quad x \neq 0. \end{cases}$$

$G(x) = \int_0^x g(s)\mathrm{d}s \to +\infty$, as $|x| \to +\infty$. (See Fig. 5) $V(x, v) = \frac{v^2}{2} + G(x)$, $\frac{d}{dt}V(x, v) \equiv 0$. So energy conserves.

By Fig. 4, every solution is periodic.

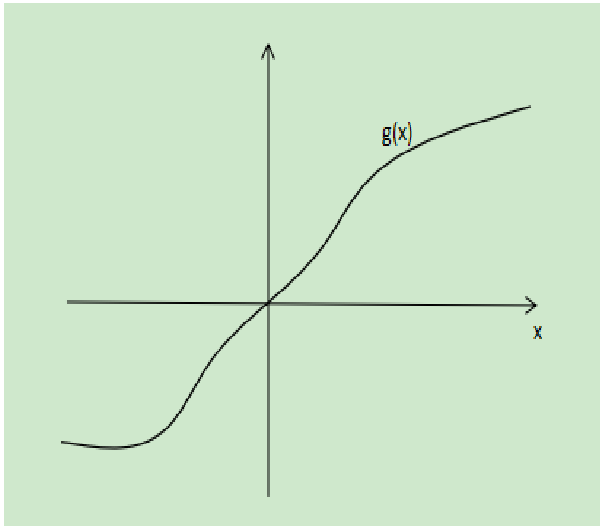

Figure 5:

Example 3: Lotka-Volterra Predator-Prey system, let $x(t) =$ prey density at time t. $y(t) =$ predator density at time t.

$$\begin{cases} x' = ax - bxy = bx(y^* - y), & y^* = \frac{a}{b}, \\ y' = cxy - dy = cy(x - x^*), & x^* = \frac{d}{c}. \end{cases}$$

where d is the predator's death rate, c is the conversion rate.

$$\begin{cases} \frac{dx}{dt} = bx(y^* - y), \\ \frac{dy}{dt} = cy(x - x^*). \end{cases}$$

Suppose $y = y(x)$,

$$\frac{dy}{dx} = \frac{cy(x - x^*)}{bx(y^* - y)},$$

then

$$\frac{x - x^*}{x}\mathrm{d}x + \frac{b}{c}\frac{y - y^*}{y}\mathrm{d}y = 0.$$

Introduce "Energy" function

$$V(x, y) = \int_{x^*}^{x} \frac{\xi - x^*}{\xi}\mathrm{d}\xi + \frac{b}{c}\int_{y^*}^{y} \frac{\xi - y^*}{\xi}\mathrm{d}\xi = (x - x^* - x^* ln\frac{x}{x^*}) + \frac{b}{c}(y - y^* - y^* ln\frac{y}{y^*}).$$

Then we have $\frac{d}{dt}V(x(t), y(t)) \equiv 0$. See Fig. 6.

Example 4: Consider L-V model[G]

$$x_i' = x_i(b_i + \sum_{j=1}^{n} a_{ij}x_j), \quad i = 1, 2, ..., n.$$

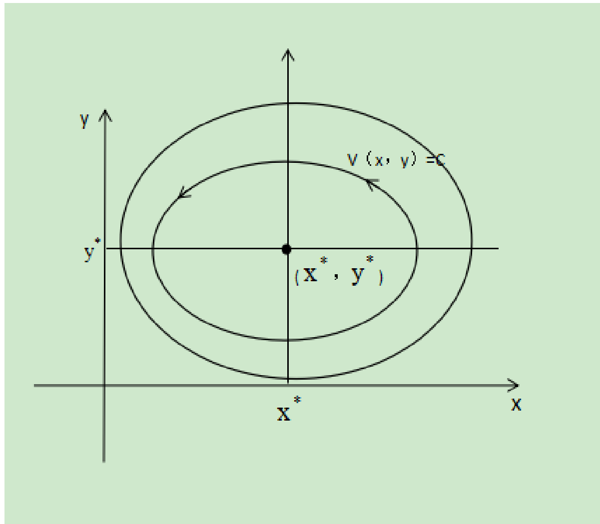

Figure 6:

B.S.Goh introduces Lyapunov function

$$V(x_1, ..., x_n) = \sum_{i=1}^{n} c_i \int_{x_i^*}^{x_i} \frac{\xi - x_i^*}{\xi} \mathrm{d}\xi,$$

where $c_i > 0$ to be determined. Let $E_c = (x_1^*, ..., x_n^*) =$ be the unique positive equilibrium, then

$$\dot{V}(x) = \frac{d}{dt} V(x_1(t), ..., x_n(t)) = \frac{1}{2}(x - x^*)(CA + A^T C)(x - x^*),$$

where $A = (a_{ij}),\ C = diag(c_1, ..., c_n)$. If $CA + A^T C$ is negative definite, then E^* is globally asymptotically stable(GAS).

Lasalle's Invariance principle[H]
Consider

$$\begin{cases} x' = f(x), & x \in G \subseteq \mathbb{R}^n, \\ x(0) = x_0. \end{cases}$$

Let $x(t, x_0)$ be a bounded solution for $t \geq 0$ and $V(x) = V(x_1, ..., x_n)$ be a Lyapunov function on G. i.e.

$$\dot{V}(x) = \frac{d}{dt} V(x_1(t), ..., x_n(t)) = \sum_{i=1}^{n} \frac{\partial V}{\partial x_i} f_i(x) \leq 0 \text{ on } G.$$

Let $S = \{x \in \bar{G} : \dot{V}(x) = 0\}$ and M be the maximal invariant set in S. Then $\lim\limits_{t \to \infty} dist(x(t, x_0), M) = 0$.

Simple Chemostat with Holling type II functional response and different removable rates[Hsu]

$$(1)\begin{cases} S' = (S^{(0)} - S)D - \sum\limits_{i=1}^{n} \dfrac{m_i S}{a_i + S} x_i, \\ x_i' = (\dfrac{m_i S}{a_i + S} - d_i) x_i, \\ S(0) \geq 0 \quad x_i(0) > 0, \quad i = 1, 2, ..., n \end{cases}$$

(H) $\lambda_1 < \lambda_2 \leq \lambda_3 \leq ... \leq \lambda_n$, $\lambda_1 < S^{(0)}$, $\lambda_i = \frac{a_i}{\frac{m_i}{d_i} - 1} > 0$. We want to the solution $(S(t), x_1(t)...x_n(t))$ satisfies (2) $\lim\limits_{t\to\infty} S(t) = \lambda_1$, $\lim\limits_{t\to\infty} x_1(t) = x_1^* = \frac{(S^{(0)} - \lambda_1)D}{d_1}$, $\lim\limits_{t\to\infty} x_i(t) = 0$ $i = 2, ..., n$.

Construct Lyapunov function:

$$(3)\ V(s, x_1...x_n) = \int_{\lambda_1}^{S} \frac{\xi - \lambda_1}{\xi} \mathrm{d}\xi + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} \mathrm{d}\xi + \sum_{i=2}^{n} c_i x_i$$

$$\begin{aligned} \dot{V}(s, x_1...x_n) &= \frac{d}{dt} V(s(t), x_1(t), ..., x_n(t)) \\ &= \frac{S - \lambda_1}{S} S'(t) + c_1 \frac{x_1 - x_1^*}{x_1} x_1'(t) + \sum_{i=2}^{n} c_i x_i'(t) \\ &= \frac{S - \lambda_1}{S} ((S^{(0)} - S)D - \frac{m_1 S}{a_1 + S} x_1 - \sum_{i=2}^{n} \frac{m_i S}{a_i + S} x_i) \\ &+ c_1 \frac{x_1 - x_1^*}{x_1} (m_1 - d_1) \frac{S - \lambda_1}{a_1 + S} + \sum_{i=2}^{n} c_i (m_i - d_i) \frac{S - \lambda_i}{a_i + S} x_i \end{aligned}$$

Choose $c_i = \frac{m_i}{m_i - d_i}$, then we have

$$\dot{V} = \frac{-(S - \lambda_1)^2 a_1}{(a_1 + S)} S\lambda_1 + \sum_{i=2}^{n} m_i (\lambda - \lambda_i) \frac{x_i}{a_i + S} \leq 0$$

Homework: Apply LaSalle's Invariance Principle to prove (2).

Remark: The Lyapunov function (3) only works for Holling-type II functional responses.

Simple Chemostat with general monotone functional responses and different removable rates.

$$(4)\begin{cases} S' = (S^{(0)} - S)D - \sum\limits_{i=1}^{n} f_i(S) x_i, \\ x_i' = (f_i(S) - d_i) x_i, \\ S(0) \geq 0 \quad x_i(0) > 0, \quad i = 1, 2, ..., n \end{cases}$$

$f_i(S)$ satisfies

(i) $f_i(0) = 0$

(ii) $f_i'(S) > 0$

(H) $\lambda_1 < \lambda_2 \le \lambda_3 \le ... \le \lambda_n,\ \lambda_1 < S^{(0)},\ f_i(\lambda_i) = d_i,\ \lambda_i > 0.$ To show (*) $\lim_{t\to\infty} S(t) = \lambda_1,\ \lim_{t\to\infty} x_1(t) = x_1^* = \frac{(S^{(0)}-\lambda_1)D}{d_1},\ \lim_{t\to\infty} x_i(t) = 0\ i = 2, ..., n$ Wolkowicz & Lu [WL] construct a Lyapunov function of the following form

$$V(S, x_1, ..., x_n) = \int_{\lambda_1}^{S} Q(\xi)\mathrm{d}\xi + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}\mathrm{d}\xi + \sum_{i=2}^{n} c_i x_i$$

where $Q(\xi)$ to be determined and c_i to be chosen.

$$\begin{aligned}\dot{V} &= Q(S)S' + \frac{x_1 - x_1^*}{x_1}(f_1(S) - d_1)x_1 + \sum_{i=2}^{n} c_i(f_i(S) - d_i)x_i \\ &= Q(S)(S^0 - S)D - \sum_{i=1}^{n} f_i(S)x_i) + (x_1 - x_1^*)(f_1(S) - d_1) + \sum_{i=2}^{n} c_i(f_i(S) - d_i)x_i \\ &= [Q(S)(S^{(0)} - S)D - x_1^*(f_1(S)) - d_1)] + x_1[(f_1(S) - d_1) - Q(S)f_1(S)] \\ &+ \sum_{1=2}^{n} x_i[c_i(f_i(S) - d_i) - f_i(S)Q(S)]\end{aligned}$$

Let $Q(S)((S^{(0)} - S)D - x_1^*(f_1(S)) - d_1)$=0, we have

$$Q(S) = \frac{x_1^*(f_1(S) - d_1)}{(S^0 - S)D}$$

we find

$$(f_1(S) - d_1)(1 - \frac{(S^0 - \lambda_1)f_1(S)}{d_1(S^0 - S)}) \le 0 \quad \text{for} \quad S > 0.$$

In order to have

$$h_i(S) = c_i(f_i(S) - d_i) - \frac{f_i(S)(f_1(S) - d_1)(S^0 - \lambda_1)}{(S^0 - S)d_1} \le 0,$$

let

$$h_i(S) = f_i(S) - d_i$$

It is easy to show that $h_i(S) \le 0$ for $\lambda_1 \le S \le \lambda_i$. Choose c_i, such that $c_i < \frac{f_i(S)(f_i(S)-d_i)(S^0-\lambda_1)}{f_i(S)-d_i} = w_i(S)$, $\lambda_i \le S \le S^{(0)}$, $c_i > w_i(S)$ for $0 < S < \lambda_1$.

By Fig. 7, $max_{0\le S\le\lambda_1} w_i(S) < c_i < min_{\lambda_i<S\le S^{(0)}} w_i(S)$. It can be shown for such c_i can be chosen under the assumption Type II: $\frac{m_i S}{a_i+S}$ and Type III: $\frac{m_i S^2}{(a_i+S)(b_i+S)}$.

(H) $\lambda_1 < \lambda_2 \le \lambda_3 \le ... \le \lambda_n,\ \lambda_1 < S^{(0)},\ f_i(\lambda_i) = d_i,\ d_i \ne D.$

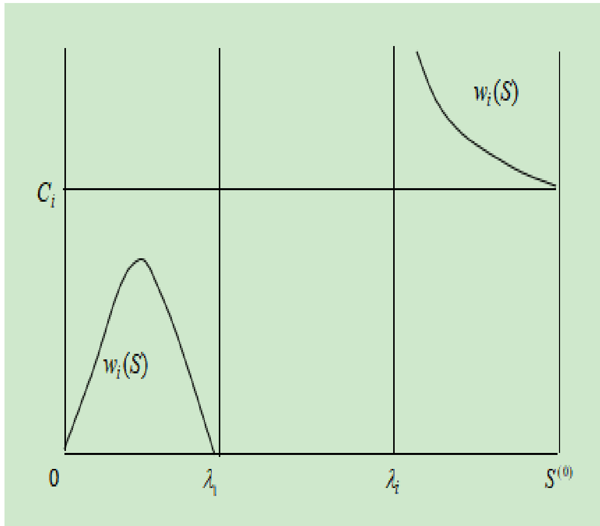

Figure 7:

Open problem: prove or disprove competitive exclusion principle holds for Simple chemostat equation (4) with general monotone functional responses and different removable rates.

Consider the following delay equation[WX]

$$\begin{cases} S'(t) = (S^{(0)} - S)D - \sum_{i=1}^{n} f_i(S)x_i, \\ x_i'(t) = -Dx_i + f_i(S(t-\tau_i))x_i(t-\tau_i), \end{cases}$$

Lemma 1.3. *(fluctuating lemma Hirsch)*
$f : [a,\infty) \to R$ is C^1, if $\lim_{t\to\infty} f(t)$ exists and $f'(t)$ is uniformly continuous(or $|f''(t)| \le M$), then $\lim_{t\to 0} f'(t) = 0$.

Lemma 1.4. *if $\liminf_{t\to\infty} f(t) < \limsup_{t\to\infty} f(t)$ then exists $t_n \uparrow \infty$ and $s_m \uparrow \infty$, such that*

$$f(t_m) \to \lim_{t\to\infty} sup f(t) \quad m \to \infty \quad f'(t_m) = 0$$

$$f(s_m) \to \lim_{t\to\infty} inf f(t) \quad m \to \infty \quad f'(s_m) = 0.$$

Main Theorem[WX] for the case of same dilution rate D: if $\lambda_1 < \lambda_j < S^{(0)}$, $= 2, ..., n$, and $\sum_{j=2}^{n}(S^{(0)} - \lambda_i) < S^{(0)} - \lambda_1$, then $(S(t), x_1(t), ..., x_n(t)) \to (\lambda_1, S^{(0)} - \lambda_1, 0, ..., 0) = E_1$

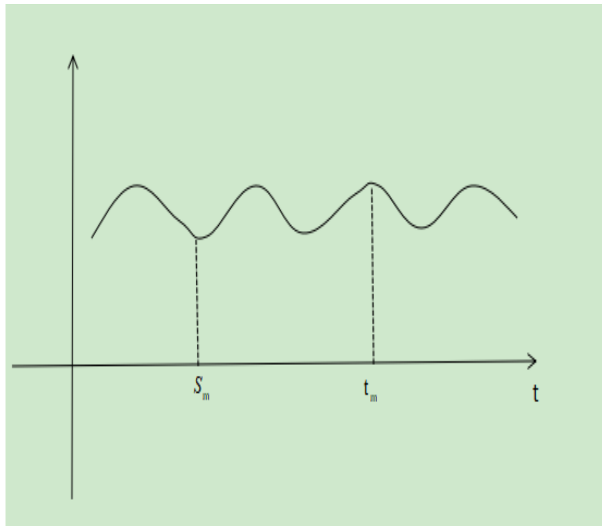

Figure 8:

For the case of different $d_i \neq D$, if $d_1 < 2D$, $\lambda_1 < \lambda_j < S^{(0)}$, $\sum_{j=2}^{n}(\frac{S^{(0)}D}{d_{min}} - \lambda_j) < \frac{S^{(0)}D}{d_{max}} - \lambda_1$ then $(S(t), x_1(t), ..., x_n(t)) \to (\lambda_1, S^{(0)} - \lambda_1, 0, ..., 0) = E_1$, where $d_{min} = min(d_1, ..., d_n)$ and $d_{max} = max(d_1, ..., d_n)$.

Open problem: Improve the work of Wolkowicz & Xia.

2 Lecture 2 Predator-Prey model

Rosenzweig-McArthur Model[HHW2]

$$\begin{aligned} Let\ \ & x(t) \text{ be prey density at time t.} \\ & y(t) \text{ be predator density at time t.} \end{aligned}$$

In the absence of predation, prey grows according to logistic equation.

$$\begin{cases} x'(t) = rx(1-\frac{x}{K}) - \frac{mx}{a+x}y \\ y'(t) = c\frac{mx}{a+x}y - dy \end{cases}$$

$$\begin{aligned} where\ \ & r \text{ is the intrinsic growth rate of prey,} \\ & K \text{ is the carrying capacity of prey,} \\ & d \text{ is the death rate of predator,} \\ & c \text{ is the conversion constant.} \end{aligned}$$

Holling Disk Model(1965)

Predator eat prey in an "attack cycle". The attack cycle includes

(i) search time T_s.

(ii) handling time h per prey item.

$$\begin{aligned} Let\ \ & N_a \text{ be the number of prey caught during the attack cycle,} \\ & T \text{ be attack cycle time} = T_s + hN_a. \end{aligned}$$

Assumption: N_a is proportional to prey density S and search time T_s.
So

$$\begin{aligned} & N_a = c \cdot S \cdot T_s. \\ & c \text{ be encounter rate per unit prey density.} \end{aligned}$$

Write $N_a = cS(T - hN_a) \Longrightarrow N_a = \frac{cST}{1+chS}$.
Let F be the feed rate per individual predator, then

$$F = \frac{N_a}{T} = \frac{cS}{1+chS} = \frac{\frac{1}{h}S}{\frac{1}{ch}+S} = \frac{V_m S}{K_m + S}.$$

Consider Predator-Prey system of Gauss Type:

$$\begin{cases} x' = xg(x) - yp(x) \\ y' = cp(x)y - dy = (cp(x)-d)y \end{cases}$$

$$\begin{aligned} & g(x) \text{ satisfies } g(x)(x-K) > 0, x \neq K, and \\ & p(x) \text{ satisfies } p(0) = 0, p'(x) > 0. \end{aligned}$$

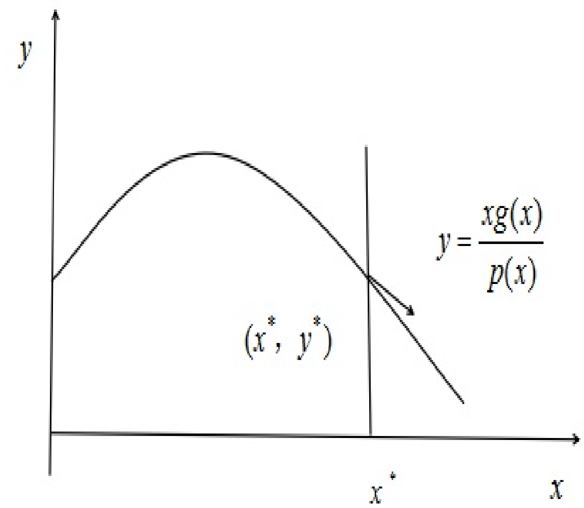

Figure 9:

Local stability analysis of equilibrium (x^*, y^*)

$$cp(x^*) = d, y^* = \frac{x^* g(x^*)}{p(x^*)}, 0 < x^* < K.$$

$$\begin{aligned} J(x^*, y^*) &= \left(\begin{array}{cc} \frac{d}{dx}(xg(x)) - yp'(x) & -p(x) \\ cp'(x)y & cp(x) - d \end{array} \right) \Bigg|_{(x,y)=(x^*,y^*)} \\ &= \left(\begin{array}{cc} (xg(x))'|_{x=x^*} - y^* p'(x^*) & -p(x^*) \\ cp'(x^*)y^* & 0 \end{array} \right). \end{aligned}$$

The eigenvalue λ of $J(x^*, y^*)$ satisfies

$$\lambda^2 - \lambda((xg(x))'|_{x=x^*} - y^* p'(x^*)) + cp'(x^*)y^* p(x^*) = 0.$$

$$Re\lambda < 0 \Leftrightarrow (xg(x))'|_{x=x^*} - y^* p'(x^*) < 0. \qquad (\bigstar)$$

The prey isocline is $y = \frac{xg(x)}{p(x)}$.
Verify.(**homework!**)

$$\frac{xg(x)}{p(x)}' |_{x=x^*} < 0 \Leftrightarrow (\bigstar) holds.$$

(x^*, y^*) is LAS(Locally asymptotically stable) if $\frac{xg(x)}{p(x)}'|_{x=x^*} < 0$. See Fig. 9.

(x^*, y^*) is unstable if $\frac{xg(x)}{p(x)}'|_{x=x^*} > 0$. See Fig. 10.

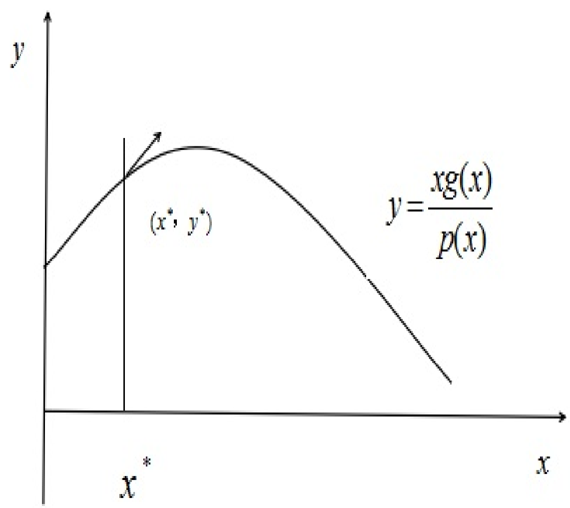

Figure 10:

For RM model,

$$\begin{cases} x'(t) = rx(1 - \frac{x}{K}) - \frac{mx}{a+x}y \\ y'(t) = (c\frac{mx}{a+x} - d)y \end{cases}$$

$$x^* = \lambda = \frac{a}{(\frac{mc}{d}) - 1}.$$

For $\frac{K-a}{2} < \lambda < K$, see Fig. 11, $E^* = (x^*, y^*)$ is locally asymptotically stable (LAS).

For $0 < \lambda < \frac{K-a}{2}$, see Fig. 12, $E^* = (x^*, y^*)$ is a unstable spiral.

Poincare Bendixson Theorem

Let $\varphi(t, x_0)$ be a bounded solution of two-dimensional autonomous system (**) for $t \geq 0$.

$$\begin{cases} x' = f(x) \\ x(0) = x_0 \end{cases} \qquad (**)$$

or

$$\begin{cases} x_1' = f_1(x_1, x_2) \\ x_2' = f_2(x_1, x_2) \end{cases}$$

then the ω-limit set $\omega(x_0) := \{p : \exists t_n \nearrow +\infty, \varphi(t_n, x_0) \to p, as\ n \to \infty\}$ satisfies

(i) $\omega(x_0)$ contains equilibrium points.

or

(ii) $\omega(x_0)$ does not contain equilibrium points.

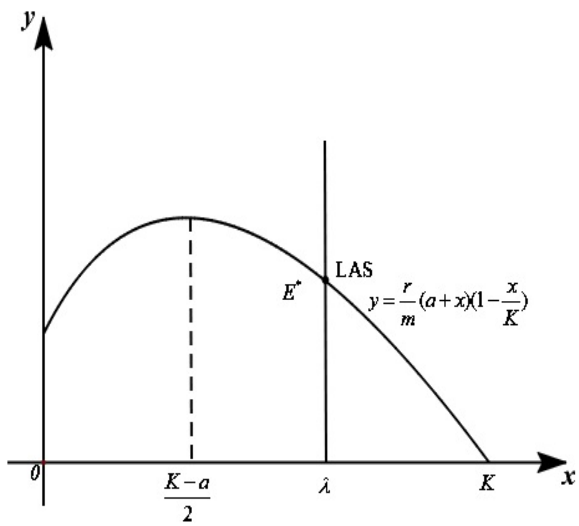

Figure 11:

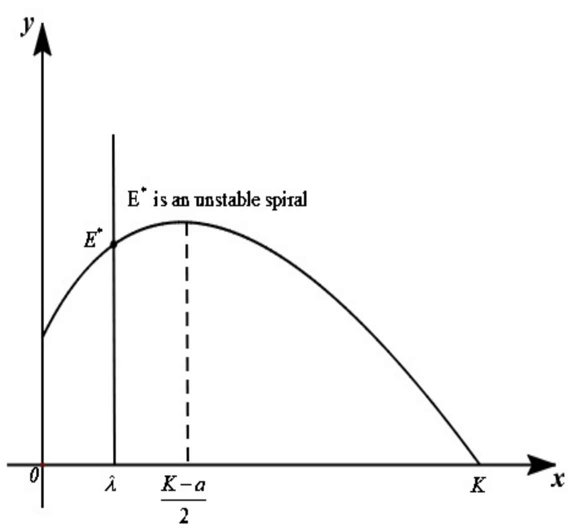

Figure 12:

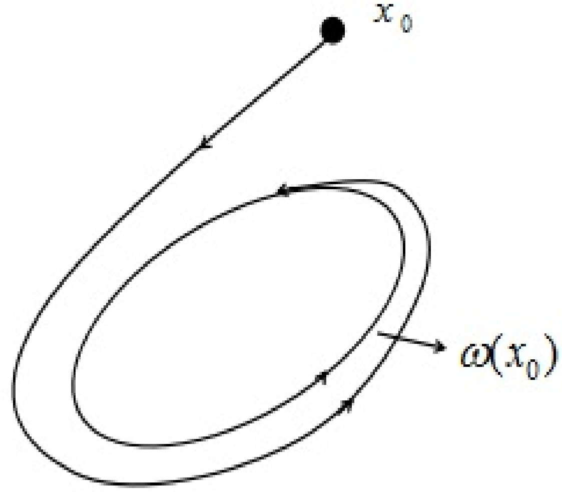

Figure 13:

In case (ii), either $\varphi(t, x_0)$ is a periodic solution or $\omega(x_0)$ is a "limit cycle"(a periodic orbit with limiting property). See Fig. 13.

We want to show global stability of (x^*, y^*), i.e.$\varphi(t, x_0) \to (x^*, y^*)$ as $t \to \infty$ for any initial point x_0 when (x^*, y^*) is LAS.

If we can eliminate the existence of periodic solution, then we can prove the global stability of $E_* = (x^*, y^*)$ which is LAS.

Negative Bendixson Criteria:

If $\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2}$ has same sign and $\not\equiv 0$ in $D \subseteq \mathbb{R}^2$, then there is no periodic solution for

$$\begin{cases} x_1' = f_1(x_1, x_2) \\ x_2' = f_2(x_1, x_2) \end{cases}$$

in D.

Dulac's Criteria:

If $\exists h(x_1, x_2) \in C^1$, s.t. $\frac{\partial(f_1 h)}{\partial x_1} + \frac{\partial(f_2 h)}{\partial x_2}$ has same sign and $\not\equiv 0$, then there is no periodic solution.

Proof. We note Green's Theorem

$$\oint_C P(x, y)\mathrm{d}x + Q(x, y)\mathrm{d}y \equiv \iint_D \left(\frac{\partial Q}{\partial x} - \frac{\partial P}{\partial y}\right)\mathrm{d}x\mathrm{d}y.$$

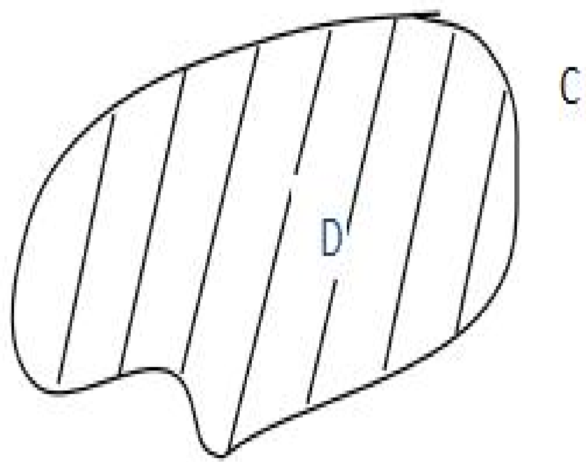

Figure 14:

See Fig. 14.

Suppose there is a periodic orbit C.

Let

$$P(x,y) = -h(x_1,x_2)f_2(x_1,x_2).$$
$$Q(x,y) = +h(x_1,x_2)f_1(x_1,x_2).$$

Then

$$\oint_C -h(x_1,x_2)f_2(x_1,x_2)\mathrm{d}x_1 + h(x_1,x_2)f_1(x_1,x_2)\mathrm{d}x_2 \equiv \iint_D (\frac{\partial(hf_1)}{\partial x_1} + \frac{\partial(hf_2)}{\partial x_2})\mathrm{d}x_1\mathrm{d}x_2 \not\equiv 0.$$

On the other hand,

$$\oint_C -h(x_1,x_2)f_2(x_1,x_2)\mathrm{d}x_1 + h(x_1,x_2)f_1(x_1,x_2)\mathrm{d}x_2 = \int_0^T -hf_2x_1' + hf_1x_2' \equiv 0,$$

a contradiction! □

Rosenzwig-McArthur Model

$$\begin{cases} x'(t) = rx(1-\frac{x}{K}) - \frac{mx}{a+x}y = f(x,y) \\ y'(t) = (c\frac{mx}{a+x} - d)y = g(x,y) \\ x(0) > 0, y(0) > 0 \end{cases}$$

By scaling, we assume $c = 1$. (**Homework!**)

Two cases:

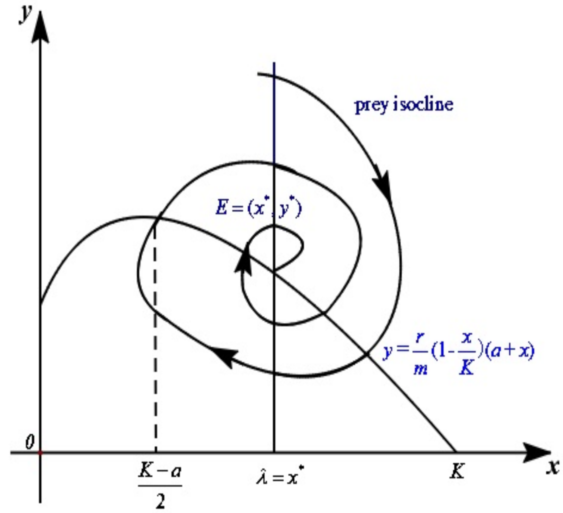

Figure 15:

(I) $\frac{K-a}{2} < \lambda < K, (x^*, y^*)$ is LAS. See Fig. 15.

(II) $0 < \lambda < \frac{K-a}{2}$, there exists a unique limit cycle. See Fig. 16.

To prove the case I: $E = (x^*, y^*)$ is GAS (globally asymptotic stable) by **Dulac's Criteria.**

Let $h(x, y) = (\frac{x}{a+x})^\alpha y^\delta$, $\alpha, \delta \in \mathbb{R}$ to be chosen.

$$\frac{\partial(fh)}{\partial x} + \frac{\partial(gh)}{\partial y} = -may^{\delta+1}x^\alpha(a+x)^{-(\alpha+2)}(\alpha+1) + ry^\delta x^\alpha(a+x)^{-(\alpha+1)}P_{\alpha,\beta}(x).$$

where $\beta = \frac{\delta+1}{r}$, $P_{\alpha,\beta}(x) = -\frac{2}{k}x^2 + (\beta(m-d) + (1 - \frac{(\alpha+2)a}{K})x + a((\alpha+1) - \beta d))$.

Choose $\alpha, \beta, \alpha \geq -1$, s.t. $P_{\alpha,\beta}(x) \leq 0$ for $x > 0$.

Compute discriminant:

$$D_\alpha(\beta) = \beta^2(m-d)^2 + \cdots \qquad (*)$$

The discriminant of (*) :

$$D(\alpha) = \cdots$$

Choose $\alpha^* > 0$, s.t.$D(\alpha^*) > 0$ and $D^*_\alpha(\beta) = 0$ has two roots $\beta_1,\ \beta_2$.

Choose $\beta^*, \beta_1 < \beta^* < \beta_2$, s.t. $D^*_\alpha(\beta^*) < 0$. (**Homework!** You have to use the condition $\frac{K-a}{2} < \lambda < K$.)

Another method: Lyapunov Method.

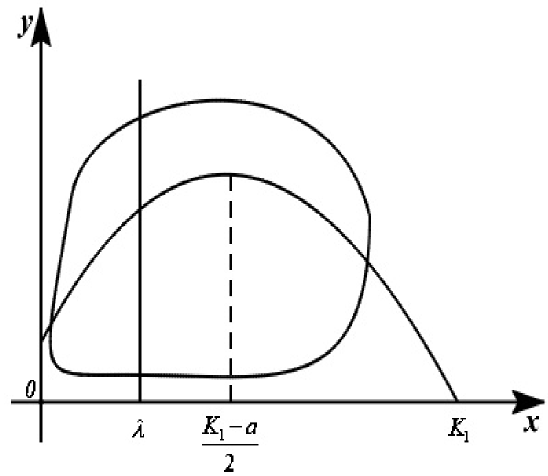

Figure 16:

Gauss-Type Predator-Prey System

$$\begin{cases} x' = xg(x) - yp(x) \\ y' = (p(x) - d)y \end{cases}$$

Construct Lyapunov function.

$$V(x,y) = \int_{x^*}^{x} \frac{p(\xi) - d}{p(\xi)} \mathrm{d}\xi + \int_{y^*}^{y} \frac{\xi - y^*}{\xi} \mathrm{d}\xi.$$

$$\begin{aligned} \dot{V}(x,y) &= \frac{p(x) - d}{p(x)}(xg(x) - yp(x)) + \frac{y - y^*}{y}(p(x) - d)y \\ &= \frac{p(x) - d}{p(x)}(xg(x) - y^*p(x) - (y - y^*)p(x)) + (y - y^*)(p(x) - d) \\ &= (p(x) - d)p(x)(xg(x) - y^*p(x)) \\ &\overset{?}{\leq} 0. \end{aligned}$$

From Fig. 17, we can see: if $x^* > \hat{x}$, then $\dot{V}(x,y) \leq 0$,this is a partial result.

Ardito and Ricciardo construct Lyapunov function in JMB (1988)[Hsu1] successfully

$$V(x,y) = y^\theta \int_{x^*}^{x} \frac{p(\xi) - d}{p(\xi)} \mathrm{d}\xi + \int_{y^*}^{y} \eta^{\theta - 1}(\eta - y^*)\mathrm{d}\eta.$$

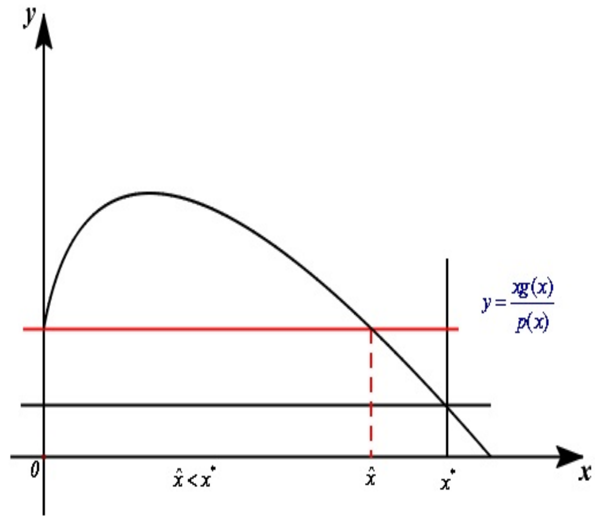

Figure 17:

Lyapunov function is of mixed type, not separable type.

θ to be chosen, $0 < \theta < 1$.

Remark: Open problem, consider the following reaction-diffusion system:

$$PDE \begin{cases} u_t = d_1 \triangle u + ug(u) - vp(u), \Omega \subseteq \mathbb{R}^n \\ v_t = d_2 \triangle v + (p(u) - d)v, \Omega \subseteq \mathbb{R}^n \\ \frac{\partial u}{\partial \nu}|_{\partial\Omega} = 0, \frac{\partial v}{\partial \nu}|_{\partial\Omega} = 0 \end{cases}$$

To show (u^*, v^*) is GAS when $(\frac{ug(u)}{p(u)})'_{u=u^*} < 0$.

Orbital Stability of Periodic Solution:

Let $x' = f(x).f : D \subseteq \mathbb{R}^n \to \mathbb{R}^n$ *and* $x^*(t)$ be a periodic solution with period T.

Consider stability of $x^*(t)$: Orbital stability of periodic orbit

$$\gamma = \{x^*(t) : 0 \le t \le T\},$$

Definition 2.1. *γ is orbitally asymptotically stable if for any $\varepsilon > 0$ there exists $\delta > 0$ s.t. $dist(x_0, \gamma) < \delta \Rightarrow dist(\varphi(t, x_0), \gamma) < \varepsilon, t \ge t_0$, for some $t_0 > 0$. See Fig 18.*

Find conditions for orbital stability of γ.

Linearization of periodic solution $x^*(t), 0 \le t \le T$. Let

$$y = x - x^*(t).$$

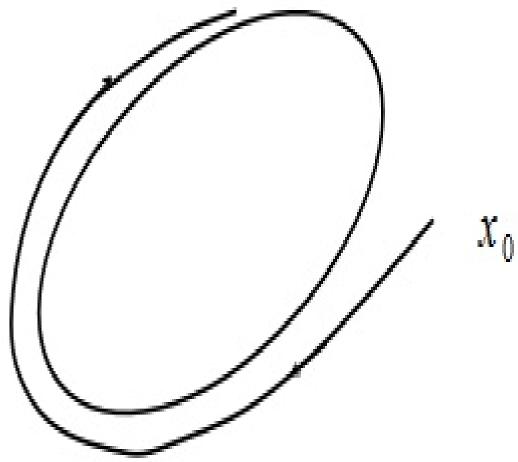

Figure 18:

Then by Taylor expansion

$$y' = x' - (x^*)'(t) = f(x) - f(x^*(t)) = D_x f(x^*(t))(x - x^*(t)) + H.O.T.$$

We obtain linearized periodic system

$$(1) \quad y' = A(t)y, \ A(t) = D_x f(x^*(t)), \ A(t) = A(t+T).$$

Consider the fundamental matrix $\Phi(t)$:

$$\begin{cases} \Phi'(t) = A(t)\Phi(t) \\ \Phi(0) = \mathrm{I} \end{cases}$$

Definition 2.2. *The eigenvalues of $\Phi(T)$ $\rho_1, \rho_2, \cdots, \rho_n$ are called Floque's multipliers of periodic system (1).*

We claim: $\rho_1 = 1$.

Proof.

$$\frac{d}{dt}x^*(t) = f(x^*(t)).$$

$$\frac{d}{dt}(\frac{d}{dt}x^*(t)) = D_x f(x^*(t))(x^*)'(t).$$

Since $\Phi(t)$ is the fundamental matrix with $\Phi(0) = \mathrm{I}$, We have $(x^*)'(t) = \Phi(t)(x^*)'(0)$.

$$(x^*)'(T) = \Phi(T)(x^*)'(0) = \Phi(T)(x^*)'(T).$$

Hence $\rho_1 = 1$ is an eigenvalues of $\Phi(T)$.

□

Theorem 2.3. [H] *If $|\rho_i| < 1, \forall\ i = 2, \cdots, n$, then $x^*(t)$ is orbitally asymptotically stable.*

From Abel's formula:

$$\det\Phi(T) = \det\Phi(0) \cdot exp(\int_0^T \text{trace}A(s)\text{d}s).$$

$$\rho_2 \cdots \rho_n = exp(\int_0^T \text{div}(D_x f(x^*(t))\text{d}t) = exp(\int_0^T (\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} + \cdots + \frac{\partial f_n}{\partial x_n})|_{x=x^*(t)}\text{d}t).$$

For the case $n = 2$,

$$\rho_2 = exp(\int_0^T (\frac{\partial f_1}{\partial x_1}(x^*(t)) + \frac{\partial f_2}{\partial x_2}(x^*(t))\text{d}t).$$

$$|\rho_2| < 1 \Longleftrightarrow \int_0^T (\frac{\partial f_1}{\partial x_1}(x^*(t)) + \frac{\partial f_2}{\partial x_2}(x^*(t))\text{d}t < 0.$$

Consider Gauss type predator-prey system:

$$\begin{cases} x' = xg(x) - yp(x), \\ y' = (p(x) - d)y. \end{cases}$$

Two Questions:

(i) global stability of $E(x^*, y^*)$, which is LAS.

(ii)Uniqueness of limit cycle, when $E(x^*, y^*)$ is unstable.

(i) strategy: To eliminate existence of periodic solution.

Proof. if not, there exist a periodic solution. To show"every"periodic solution is orbitally asymptotically stable. Then, the periodic orbit is unique. It is impossible to have a stable limit cycle "enclosed" a stable equilibrium. As Fig. 19 shows below and we obtain: □

Theorem 2.4. ***(Weak Negative Bendixson Criteria)***
If for every periodic orbit $(x^*(t))_{t=0}^{t=T}$,

$$\int_0^T \frac{\partial f}{\partial x}(x^*(t)) + \frac{\partial g}{\partial y}(x^*(t))dt < 0,$$

then (x^*, y^*) is GAS.

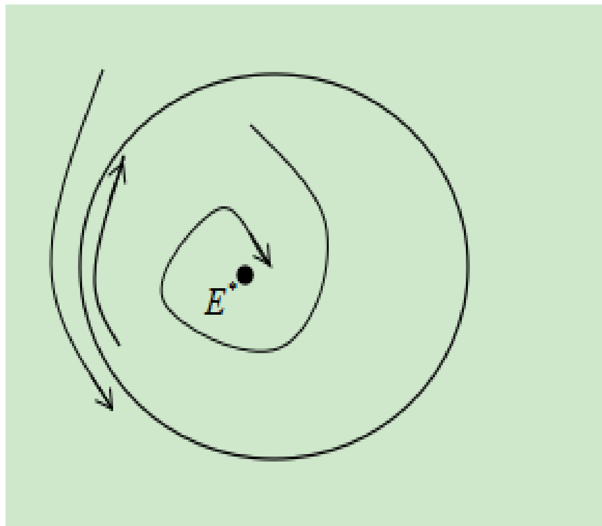

Figure 19:

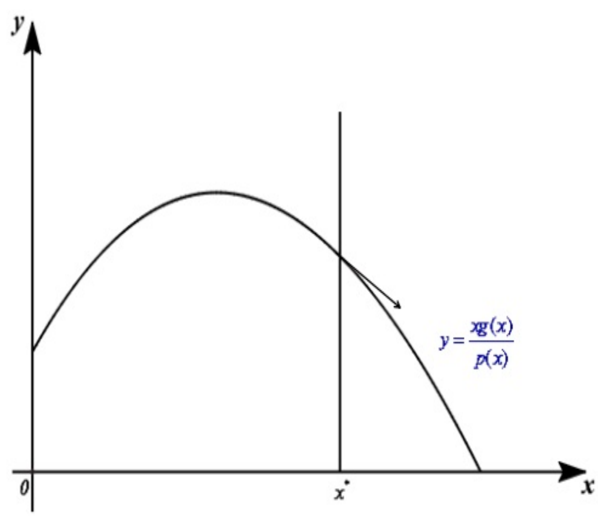

Figure 20:

Assume (x^*, y^*) is LAS, then $(\frac{xg(x)}{p(x)})'|_{x=x^*} < 0$(see Fig. 20),and

$$\frac{d}{dx}(\frac{xg(x)}{p(x)}) = \frac{p(x)(xg(x))' - (xg(x))p'(x)}{(p(x))^2},$$

let

$$f(x) = \frac{d}{dx}(xg(x)) - \frac{(xg(x))p'(x)}{p(x)},$$

then (x^*, y^*) is LAS iff $f(x^*) < 0$.

Theorem 2.5. *If* $\frac{f(x)-f(x^*)}{p(x)-p(x^*)} \in C^1$ & $\frac{d}{dx}(\frac{f(x)-f(x^*)}{p(x)-p(x^*)}) \leq 0$, $\forall 0 \leq x \leq K$, *then* (x^*, y^*) *is GAS.*

Proof. Suppose $(x(t), y(t))$ is a periodic solution of period T.

$$\Delta = \int_0^T ((xg(x))' - yp'(x)) + (p(x) - d)dt$$

Since

$$\int_0^T \frac{y'}{y} = \int_0^T (p(x) - d) = 0,$$

then

$$\Delta = \int_0^T ((xg(x))' - yp'(x))dt.$$

Since

$$0 = \int_0^T \frac{p'(x)}{p(x)}x' = \int_0^T xg(x)\frac{p'(x)}{p(x)} - \int_0^T p'(x)y,$$

then

$$\Delta = \int_0^T f(x)dt = \int_0^T f(x^*)dt + \int_0^T (f(x) - f(x^*))dt$$

we obtain $\int_0^T f(x^*)dt < 0$, we need to show $\int_0^T (f(x) - f(x^*))dt < 0$.

$$\begin{aligned}\int_0^T (f(x) - f(x^*))dt &= \int_0^T \frac{f(x(t)) - f(x^*)}{(p(x(t)) - p(x^*))}((p(x(t)) - p(x^*))dt \\ &= \oint \frac{f(x) - f(x^*)}{p(x) - p(x^*)}\frac{1}{y}dy \\ &= \iint_\Omega \frac{1}{y}\frac{d}{dx}(\frac{f(x) - f(x^*)}{p(x) - p(x^*)})dxdy < 0 \text{ (Green's Theorem)}\end{aligned}$$

□

And we can check for the case $p(x) = \frac{mx^n}{a+x^n}$.

Homework: To show (x^*, y^*) is GAS, if $\frac{K-a}{2} < \lambda = x^* < K$, by Theorem2.5.

(ii) Uniqueness of limit cycle[CHL]:

$$\begin{cases} S' = rS(1 - \frac{S}{K}) - (\frac{m}{y})\frac{Sx}{a+S} = \frac{m}{y}\frac{S}{a+S}(f(S) - x) = g(S, x), \\ x' = (\frac{mS}{a+S} - d)x = h(S, x) = (m - d)\frac{(S-\lambda)x}{a+S}. \end{cases}$$

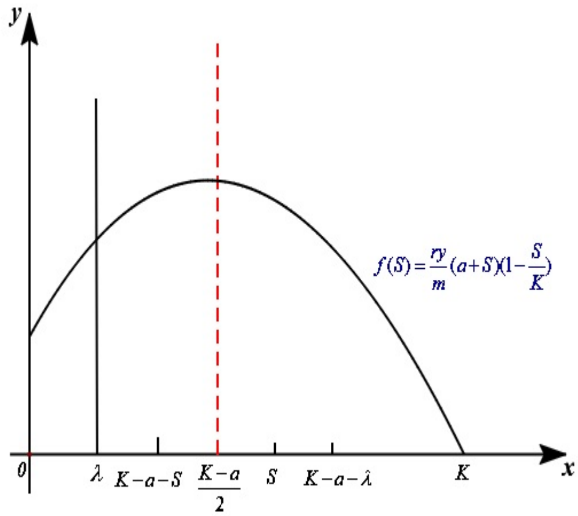

Figure 21:

Proof. To show the Floque multiple ρ_2, satisfies $\rho_2 < 1$, we need to show

$$\oint \frac{\partial g}{\partial S} + \frac{\partial h}{\partial x} = \oint \frac{\partial g}{\partial S} = \oint \frac{m}{y}\frac{Sf'(S)}{a+S} + \frac{m}{y}\frac{a(f(S)-x)}{(a+S)^2}$$

From Fig. 21, we can find that for $\frac{K-a}{2} < S < K - a - \lambda$,

$$f(S) = f(K-a-S),$$
$$f'(S) = -f'(K-a-S)$$

Since

$$0 = \int_0^T \frac{aS'}{a+S} = \int_0^T \frac{m}{y}\frac{a(f(S)-x)}{(a+S)^2}$$

then

$$\oint \frac{\partial g}{\partial S} + \frac{\partial h}{\partial x} = \oint \frac{\partial g}{\partial S} = \oint_\Gamma \frac{m}{y}\frac{Sf'(S)}{a+S}$$

Since $S'(t) = \frac{m}{y}\frac{S}{a+S}(f(S)-x)$, so $\frac{S'(t)}{f(S)-x} = \frac{m}{y}\frac{S}{a+S}$. To show

$$\oint \frac{\partial g}{\partial S} + \frac{\partial h}{\partial x} = \oint \frac{\partial g}{\partial S} = \oint_\Gamma \frac{m}{y}\frac{Sf'(S)}{a+S} < 0$$

By Fig. 22, we obtain

$$\oint_\Gamma \frac{m}{y}\frac{Sf'(S)}{a+S} = \int_{\widehat{AP}} + \int_{\widehat{PRQ}} + \int_{\widehat{QB}} + \int_{\widehat{BQ'}} + \int_{\widehat{Q'LP'}} + \int_{\widehat{P'A}}$$

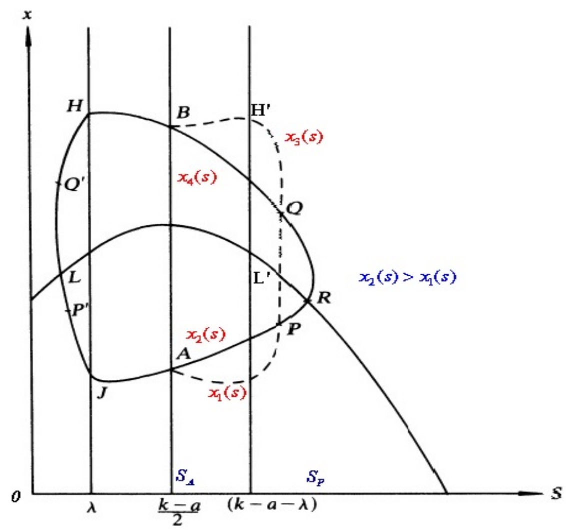

Figure 22:

$$
\begin{aligned}
(\int_{\widehat{P'A}} + \int_{\widehat{AP}})\frac{m}{y}\frac{Sf'(S)}{a+S} &= \int_{S_P}^{S_A} \frac{f'(S)}{f(S)-x_1(S)} + \int_{S_A}^{S_P} \frac{f'(S)}{f(S)-x_2(S)} \\
&= \int_{S_A}^{S_P} \frac{f'(S)}{f(S)-x_2(S)}ds + \int_{S_A}^{S_P} \frac{f'(K-a-S)}{f(K-a-S)-x_1(K-a-S)} \\
&= \int_{S_A}^{S_P} f'(S)[\frac{x_2(s)-x_1(K-a-S)}{(f(S)-x_2(S))(f(S)-x_1(K-a-S))}] < 0
\end{aligned}
$$

where $x_2(S) > x_1(K-a-S)$ for $S_A < S < S_p$,and $f'(S) < 0$ for $S_A < S < S_p$.

Similarly

$$
[\int_{\widehat{QB}} + \int_{\widehat{BQ'}}](\frac{m}{y}\frac{Sf'(S)}{a+S})dt = \int_{S_B}^{S_Q} f'(S)[\frac{x_3(K-a-S)-x_4(S)}{(x_4(S)-f(S))(x_3(K-a-S)-f(S))}]ds < 0
$$

Since

$$
x'(t) = x(m-d)\frac{S-\lambda}{a+S}
$$

and

$$
\frac{1}{m-d}\frac{a+S}{(S-\lambda)x}dx = dt
$$

then based on Green's Theorem, we have

$$\int_{\widehat{Q'LP'}}(\frac{m}{y}\frac{Sf'(S)}{a+S})dt = \frac{m}{y}\frac{1}{m-d}\int_{\widehat{Q'LP'}}\frac{Sf'(S)}{x(S-\lambda)}dx$$
$$= \frac{m}{y}\frac{1}{m-d}[\int_{\widehat{Q'LP'}}+\int_{\widehat{P'Q'}}+\int_{\widehat{Q'P'}}]\frac{Sf'(S)}{x(S-\lambda)}dx$$
$$= \frac{m}{y}\frac{1}{m-d}\iint_{\Omega}-\frac{1}{x}\frac{\frac{r}{K}[2(S-\lambda)^2+\lambda(K-a-2\lambda)]}{(S-\lambda)^2}dsdx$$
$$+\int_{\widehat{Q'P'}}\frac{Sf'(S)}{x(S-\lambda)}dx$$
$$< \frac{m}{y}\frac{1}{m-d}\int_{x_{p'}}^{x_{Q'}}\frac{S_1(x)f'(S_1(x))}{x(\lambda-S_1(x))}dx$$

Simiarly,we have

$$\int_{\widehat{PRQ}}(\frac{m}{y}\frac{Sf'(S)}{a+S})dt = \frac{m}{y}\frac{1}{m-d}[\iint_{\Omega}-\frac{1}{x}\frac{\frac{r}{K}[2(S-\lambda)^2+\lambda(K-a-2\lambda)]}{(S-\lambda)^2}dsdx$$
$$+\int_{\widehat{PQ}}\frac{Sf'(S)}{x(S-\lambda)}dx]$$
$$< \frac{m}{y}\frac{1}{m-d}\int_{x_p}^{x_Q}\frac{S_2(x)f'(S_2(x))}{x(S_2(x))-\lambda}dx$$

Then

$$(\int_{\widehat{Q'LP'}}+\int_{\widehat{PRQ}})\frac{m}{y}\frac{Sf'(S)}{a+S}dt < \frac{m}{y}\frac{1}{m-d}\int_{x_{P'}}^{x_{Q'}}\frac{S_1(x)f'(S_1(x))}{x(\lambda-S_1(x))}dx$$
$$-\frac{m}{y}\frac{1}{m-d}\int_{x_{P'}}^{x_{Q'}}\frac{(K-a-S_1(x))f'(S_1(x))}{x(K-a-\lambda-S_1(x))}dx$$
$$= \frac{m}{y}\frac{1}{m-d}\int_{x_{P'}}^{x_{Q'}}\frac{f'(S_1(x))}{x}\frac{G(S_1(x))}{\lambda-S_1(x)(K-a-\lambda-S_1(x))}dx$$
$$< \frac{m}{y}\frac{1}{m-d}\int_{x_p}^{x_Q}\frac{S_2(x)f'(S_2(x))}{x(S_2(x))-\lambda}dx$$

and

$$G(S') = (S-\lambda)(\lambda-S')(\frac{S'}{\lambda-S'}-\frac{S}{S-\lambda}).$$

Let $S = K-a-S'$,we have

$$\begin{array}{ll} S_1(x) \le max\{S_{P'}, S_{Q'}\} \le S_-, & x_{P'} \le x \le x_{Q'} \\ G(S_1(x)) \le 0, & x_{P'} \le x \le x_{Q'}x. \end{array}$$

then

$$(\int_{\widehat{Q'LP'}}+\int_{\widehat{PRQ}})(\frac{m}{y}\frac{Sf'(S)}{a+S})dt < 0.$$

So

$$\int_\Gamma D_1 v(g,h)dt < 0$$

□

Uniqueness of limit cycle
Method of generalized Lienard equations.

Lienard equations:

$$x'' + f(x)x' + g(x) = 0.$$

Example: Van der pol equation

$$f(x) = k(x^2 - 1), g(x) = x.$$

Example: Cartwright and Littlewood studied van der pol equation with periodic perturbation

$$x'' + k(x^2 - 1)x' + x = b \sin \omega t.$$

S.Smale discovered horse-shoe structure in chaotic dynamics from this equation.

Write Lienard equation in Lienard form[H]:

$$\begin{cases} \frac{\mathrm{d}x}{\mathrm{d}t} = -y - F(x), \ F(x) = \int_0^x f(\xi)\mathrm{d}\xi. \\ \frac{\mathrm{d}y}{\mathrm{d}t} = g(x), \qquad G(x) = \int_0^x g(\xi)\mathrm{d}\xi. \end{cases}$$

Levinson.Smith theorem proves uniqueness of limit cycle. Assume there are two limit cycle. To get a contradiction! (Using some symmetry!)(See[H])

Generalized Lienard Equation[Z]:

$$\begin{cases} \frac{\mathrm{d}x}{\mathrm{d}t} = -\varphi(y) - F(x) \\ \frac{\mathrm{d}y}{\mathrm{d}t} = g(x) \end{cases} \qquad (\star)$$

Theorem 2.6. [Z] *Assume*

(i) $xg(x) > 0, \ x \neq 0, \ G(+\infty) = G(-\infty) = +\infty$. $G(x) = \int_0^x g(\xi)\mathrm{d}\xi$.

(ii) $\frac{F'(x)}{g(x)}$ *is non-decreasing on* $(-\infty, 0), (0, +\infty)$, $\frac{F'(x)}{g(x)} \neq$ *constant in neighborhood of* $x = 0$.

(iii) $y\varphi(y) > 0, \ y \neq 0, \ \varphi(y)$ *is non-decreasing.* $\varphi(-\infty) = -\infty, \ \varphi(+\infty) = +\infty$. $\varphi(y)$*has right and left derivative at*$x = 0$ *which are non-zero in case* $F'(0) = 0$.

Then the system $\star$ *has at most one limit cycle.*

In 1988, Kuang Yang and Freedman prove uniqueness of limit cycle for Gauss-type Predator-Prey System by reducing it to generalized Lienard equation[KF].

Consider Predator-Prey System:

$$\begin{cases} \frac{\mathrm{d}x}{\mathrm{d}t} = \phi(x)(F(x) - \pi(y)) \\ \frac{\mathrm{d}y}{\mathrm{d}t} = p(x)\psi(x) \end{cases}$$

Example: Gauss-type predator-prey system

$$\begin{cases} \pi(y) = y, \ \phi(x) = p(x). \\ F(x) = \frac{xg(x)}{p(x)} = \text{prey isocline.} \\ p(y) = y, \ \psi(x) = p(x) - p(x^*). \end{cases}$$

Theorem 2.7. *Assume*

(i) $\varphi(0) = \pi(0) = p(0) = 0. \phi'(x) > 0, p'(y) > 0, \pi'(y) > 0, \pi(+\infty) = +\infty.$

(ii) $\psi(x^*) = 0, K > x^*, F(K) = 0, (x - K)F(x) < 0, \forall x \neq K.$

(iii) $\frac{-F'(x)\phi(x)}{\psi(x)}$ *is non-decreasing for* $-\infty < x < x^*, x^* < x < +\infty.$

Then there is at most one limit cycle.

Proof. Let (x^*, y^*) be the equilibrium.

Consider change of variable $(x, y) \to (u, v)$.

$$x = \xi(u) + x^*$$

$$y = \eta(v) + y^*$$

$\xi(u), \eta(v)$ to be determined.

Then

$$\begin{cases} \frac{\mathrm{d}u}{\mathrm{d}t} = \frac{1}{\xi'(u)}\phi(\xi(u) + x^*)(F(\xi(u) + x^*) - \pi(\eta(v) + y^*)) \\ \frac{\mathrm{d}v}{\mathrm{d}t} = \frac{1}{\eta'(v)}p(\eta(v) + y^*)\psi(\xi(u) + x^*) \end{cases}$$

Set

$$\begin{cases} \xi'(u) = \phi(\xi(u) + x^*) \\ \xi(0) = 0 \end{cases}$$

$$\begin{cases} \eta'(v) = p(\eta(v) + y^*) \\ \eta(0) = 0 \end{cases}$$

(See Fig. 23, 24.)

Write

$$\begin{aligned} \frac{\mathrm{d}u}{\mathrm{d}t} &= -[\pi(\eta(v) + y^*) - y^*] - [-F(\xi(u) + x^*) + y^*] \\ &= -\Phi(v) - \hat{F}(u) \\ &= p(x) \\ \frac{\mathrm{d}v}{\mathrm{d}t} &= \psi(\xi(u) + x^*) = g(u) \end{aligned}$$

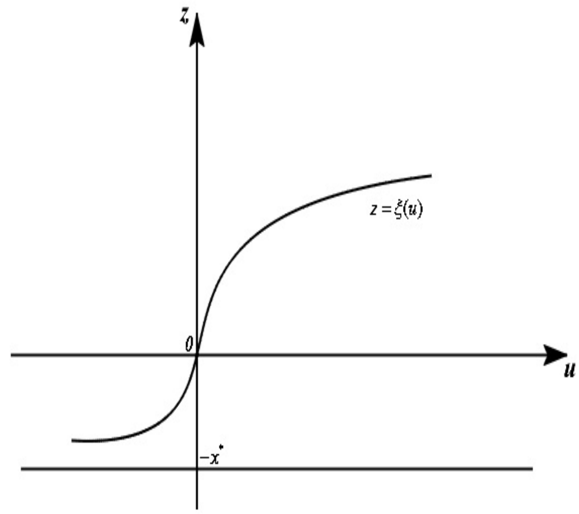

Figure 23:

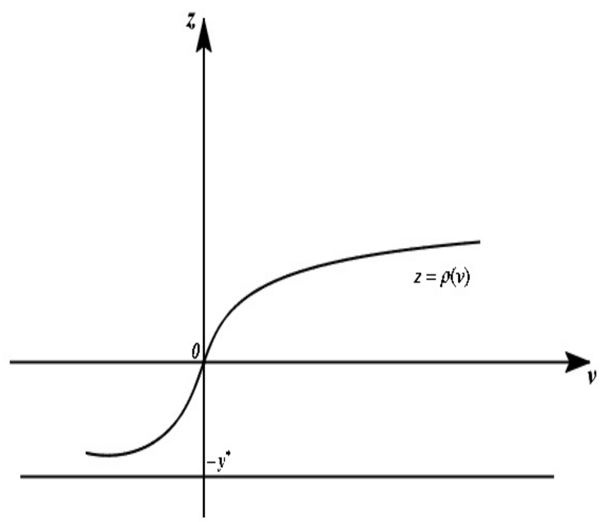

Figure 24:

Check: The conditions in generalized Lienard equations.

$$ug(u) = u\psi(\xi(u) + x^*) = u(p(\xi(u) + x^*) - p(x^*)) > 0, u \neq 0.$$

$$G(u) = \int_0^u g(s)\mathrm{d}s \to +\infty \text{ as } |u| \to +\infty.$$

$$v\Phi(v) = v(\pi(\eta(v) + y^*) - y^*) > 0, v \neq 0.$$

Check: $\frac{F'(u)}{g(u)}$ is non-decreasing on $(-\infty, 0), (0, +\infty)$.

$$\hat{F}'(u) = -F'(\xi(u) + x^*)\xi'(u) = -F'(\xi(u) + x^*)\phi(\xi(u) + x^*).$$

$$\frac{\hat{F}'(u)}{g(u)} = \frac{-F'(\xi(u) + x^*)\phi(\xi(u) + x^*)}{\psi(\xi(u) + x^*)}$$

is non-decreasing in u, since $\frac{-F'(u)\phi(x)}{\psi(x)}$ in nondecreasing in x, $-\infty < x < x^*$, $x^* < x < \infty$. $\therefore$ (iii) holds.

□

Example: To prove uniqueness of limit cycle for RM model.

Here

$$F(x) = \frac{r}{m}(a + x)(1 - \frac{x}{K}) \text{ be the prey isocline.}$$

$$\phi(x) = \frac{mx}{a + x} = p(x)$$

$$\psi(x) = \frac{mx}{a + x} - d = (m - d)\frac{x - x^*}{a + x}$$

Homework: To show $\frac{-F'(x)\phi(x)}{\psi(x)}$ is non-decreasing on $(-\infty, x^*), (x^*, +\infty)$. Compute $(\frac{-F'(x)\phi(x)}{\psi(x)})'$.

Example: See [Huang][Hu]

$$p(x) = \frac{mx^n}{a + x^n} = \phi(x)$$

Then the system

$$\begin{cases} x' = rx(1 - \frac{x}{K}) - \frac{mx^n}{a+x^n}y, \\ y' = (\frac{mx^n}{a+x^n} - d)y. \end{cases}$$

has a unique limit cycle.

Paradox of enrichment:

See Fig. 25.

Increase K to K_1, the equilibrium become unstable. Then population of prey and predator become extinct. See Fig. 26.

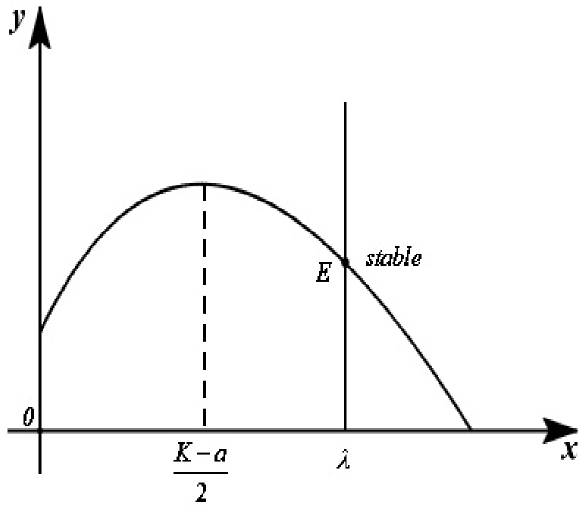

Figure 25:

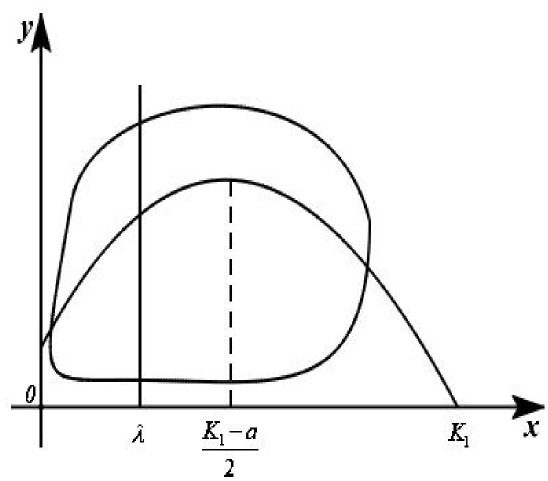

Figure 26:

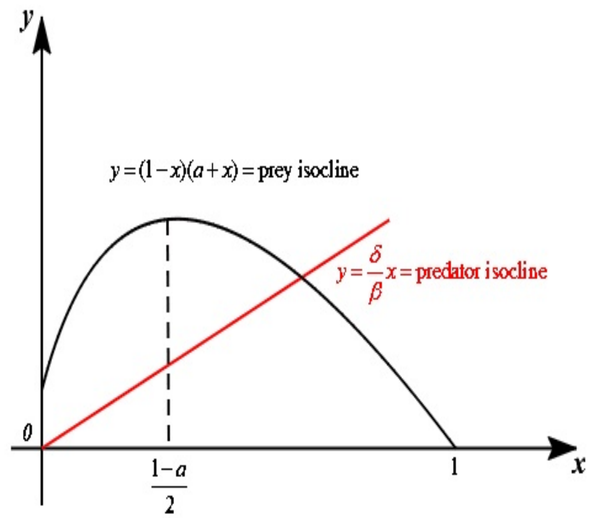

Figure 27:

Consider Holling-Tanner Model[HHw]:

$$\begin{cases} x' = rS(1-\dfrac{x}{K}) - \dfrac{mx}{a+x}y, \\ y' = \delta y(1-\dfrac{y}{hx}) \qquad\qquad h>0. \end{cases}$$

Assume predator grows according to logistic equation with intrinsic growth rates and carrying capacity proportional to the population density of prey.

Homework: Convert the above equation into the following equation.

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{x}{a+x}y, \\ \dfrac{dy}{dt} = y(\delta - \beta\dfrac{y}{x}). \end{cases}$$

(See Fig. 27)Next,we reduced it to Gauss-type Predator-Prey system, let

$$(x,y) \to (x,u)$$

$$u = yl(x), \quad l(x) = \left(\frac{1-x}{x}\right)^{\delta}$$

then, we obtain

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{x}{a+x}\frac{u}{l(x)}, \\ \dfrac{du}{dt} = \dfrac{u^2\beta}{xl(x)(1-x)(a+x)}(x+\dfrac{a}{x^*})(x-x^*). \end{cases}$$

From Fig. 28, we have the following cases:

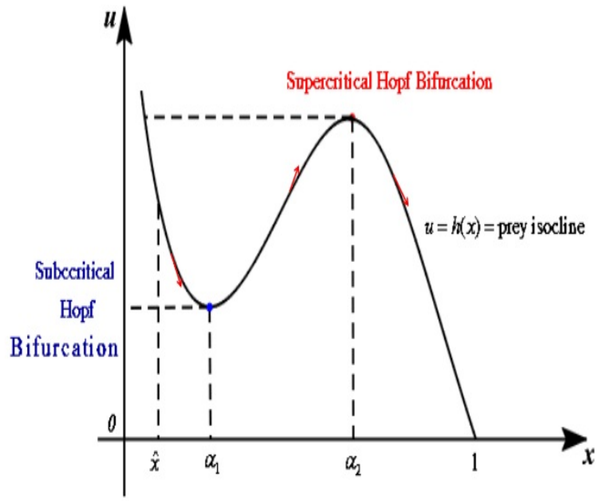

Figure 28:

(i) $0 < x^* < \hat{x}$, we can show(x^*, u^*) is GAS by Lyapunov function.

(ii) $\hat{x} < x^* < \alpha_1$, $E^* = (x^*, u^*)$ is LAS, but we don't know how to prove it is GAS.(open problem 1)

(iii) $\alpha_1 < x^* < \alpha_2, E^* = (x^*, u^*)$ is unstable, we only have partial results[HHz] on uniqueness of limit cycle.(open problem 2)

(iv) $\alpha_2 < x^* < 1$ we prove E^* is GAS by Dulac criteria.

We note that supercritical Hopf bifurcation occurs at $x^* = \alpha_2$ and subcritical Hopf bifurcation occurs at $x^* = \alpha_1$.

Ratio-dependence Predator-Prey model[HHK] **(see Fig.29):**

$$\begin{cases} x' = ax(1 - \dfrac{x}{K}) - \dfrac{czy}{m+z}, \\ y' = y(f\dfrac{z}{m+z} - d), \\ z = \frac{x}{y}. \end{cases}$$

where x is the prey density, y is the predator density. we obtain the following system:

$$\begin{cases} x' = ax(1 - \dfrac{x}{K}) - \dfrac{cxy}{my+x}, \\ y' = y(\dfrac{fx}{my+z} - d). \end{cases}$$

we consider the predator isocline: $f(x) = (my + x)d$, then $y = \frac{f-d}{md}x$. (see Fig.30)

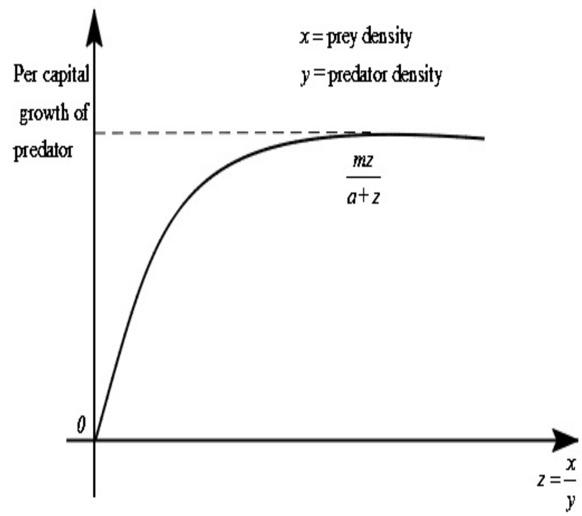

Figure 29:

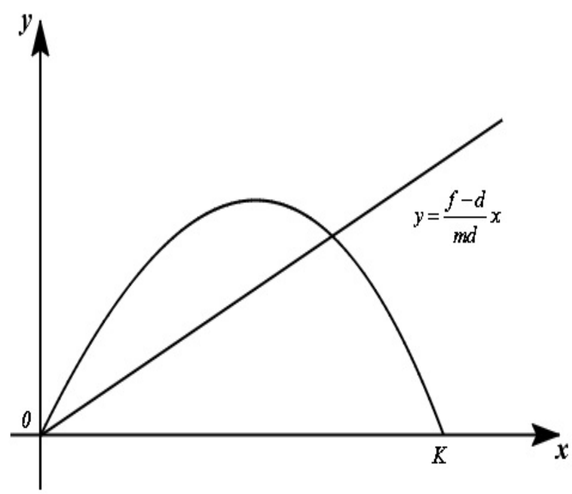

Figure 30:

Scaling: $t \to at$, $x \to \frac{x}{K}$, $, y \to \frac{my}{K}$, we obtain

$$\begin{cases} x' = x(1-x) - \dfrac{sxy}{x+y}, & s = \dfrac{c}{ma}, \\ y' = \delta y(-r + \dfrac{x}{x+y}), & \delta = \dfrac{f}{a} \quad r = \dfrac{d}{f}. \end{cases}$$

Then we use change of variable $(x, y) \to (u, y)$, and $u = \frac{x}{y}$, we obtain:

$$\begin{cases} u'(t) = g(u) - \varphi(u)y, \\ y'(t) = \psi(u)y, \\ u(0) = u_0 > 0, \quad y(0) = y_0 > 0. \end{cases}$$

then

$$\begin{cases} g(u) = \dfrac{u(1 + \delta r - s + (1 + \delta r - \delta)u)}{u+1}, \\ \varphi(u) = u^2, \\ \psi(u) = \delta(\dfrac{u}{u+1} - r). \end{cases}$$

Next, we consider the prey isocline:

$$y = h(u) = \frac{g(u)}{\varphi(u)} = \frac{(1 + \delta r - s + (1 + \delta r - \delta)u)}{u(u+1)},$$

let

$$A = 1 + \delta r - \delta$$

$$B = 1 + \delta r - s$$

we obtain two equilibrium points: $E_0 = (0, 0)$, $E_1 = (\theta_0, 0)$. if $AB < 0$, we assume that $E^* = (u^*, y^*), u^* = \frac{r}{1-r}$. The stability analysis is the following:

Consider the most interesting case is $A > 0, B < 0$. In Fig. 31, we assume the stable manifold Γ of E_1 intersect the prey iscoline $y = h(u)$. Then Γ connects E_1 and E^*.

If Γ does not intersect prey isocline, then there two cases.

Case 1: $\theta_1 < u^*$

E^* is LAS. Γ separates u-y plane into two regions Ω_1 and Ω_2. If $(u_0, y_0) \in \Omega_1$, then $(u(t), y(t)) \to E_0$ as $t \to \infty$. If $(u_0, y_0) \in \Omega_2$, then $(u(t), y(t)) \to E^*$ as $t \to \infty$. (See Fig. 32)

Case 2: $\theta_0 < u^* < \theta_1$

E^* is unstable surrounded by a unique limit cycle Γ. If $(u_0, y_0) \in \Omega_1$, then $(u(t), y(t)) \to E_0$ as $t \to \infty$. If $(u_0, y_0) \in \Omega_2$, then $(u_0, y_0)) \neq E^*$, then $(u(t), y(t))$ approach the limit cycle Γ. (See Fig. 33)

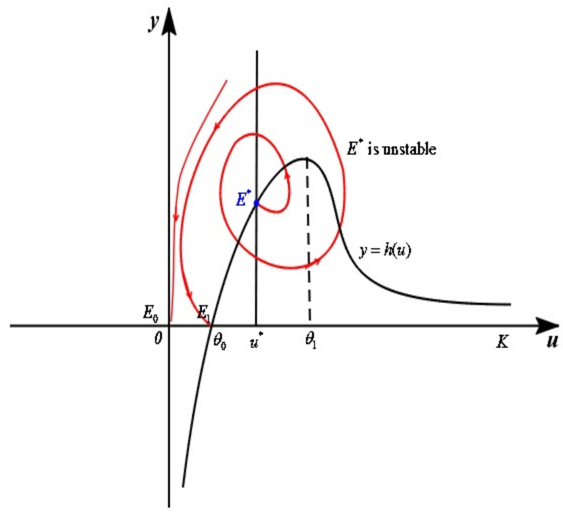

Figure 31:

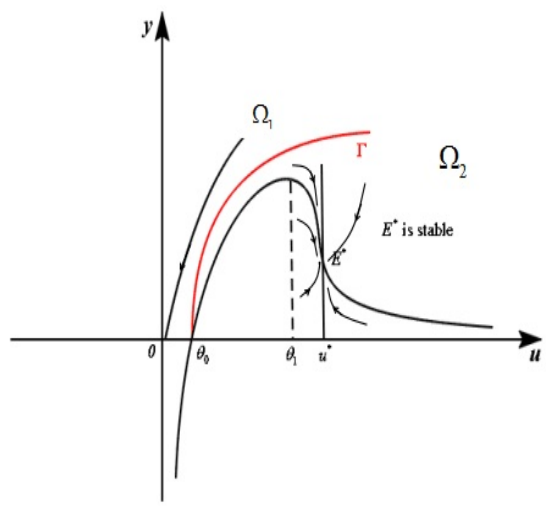

Figure 32:

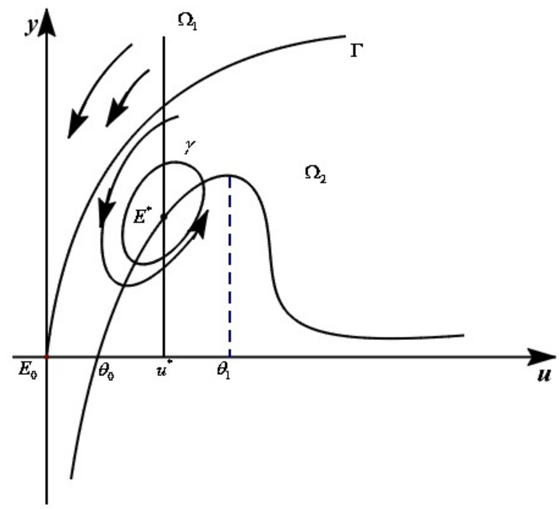

Figure 33:

3 Lecture 3 Two Predators Compete for a Single Renewable Prey

Consider the equation

$$\begin{cases} S'(t) = rS(t)(1-\frac{S(t)}{K}) - \frac{1}{y_1}\frac{m_1 S}{a_1+S}x_1 - \frac{1}{y_2}\frac{m_2 S}{a_2+S}x_2 \\ x_1'(t) = (\frac{m_1 S}{a_1+S} - d_1)x_1, \\ x_2'(t) = (\frac{m_2 S}{a_2+S} - d_2)x_2, \\ x_1(0) > 0, x_2(0) > 0, S(0) > 0 \end{cases}$$

where $S(t)$ is the density of prey at time t and $x_i(t)$ is the density of i-th predator at time t. i=1,2. We may assume $y_1 = y_2 = 1$ by scaling.

Differential inequalities: Let $f: \ R \times R \to R, \ f = f(t,x)$. Assume x(t) satisfies

$$\begin{cases} x'(t) \le f(t, x(t)), \quad t \ge t_0 \\ x(t_0) \le x_0. \end{cases}$$

let $\varphi(t)$ be solution of

$$\begin{cases} z' = f(t,z), \quad t \ge t_0 \\ z(t_0) = x_0. \end{cases}$$

Then $x(t) \le \varphi(t_0)$ for $t \ge t_0$.

Lemma 3.1. *The solution* $(S(t), x_1(t), x_2(t))$ *is positive and bounded.*

Proof. **Homework:** $(S(t), x_1(t), x_2(t))$ is positive for $t \ge 0$.
Now,we prove the solution is bounded.

$$\frac{dS}{dt} + \frac{dx_1}{dt} + \frac{dx_2}{dt} = rS(1-\frac{S}{K}) - d_1x_1 - d_2x_2.$$

Since $S'(t) \le rS(t)(1-\frac{S(t)}{K})$ and $S(t) \le K+\varepsilon$ for $t \ge t_\varepsilon > 0$. Let $d_{min} = min(d_1, d_2)$. Then

$$\begin{aligned} S'(t) + x_1'(t) + x_2'(t) &\le r(K+\varepsilon) - d_1x_1 - d_2x_2 \\ &\le r(K+\varepsilon) - d_{min}(S+x_1+x_2) + d_{min}S \\ &\le [r(K+\varepsilon) + d_{min}(K+\varepsilon)] - d_{min}(S+x_1+x_2). \end{aligned}$$

Then from differential inequality, we have

$$S(t) + x_1(t) + x_2(t) \le \frac{r(K+\varepsilon) + d_{min}(K+\varepsilon)}{d_{min}}, \ t \ge t_\epsilon$$

So the solution is bounded. □

To show extinction of predators, we make $\frac{1}{y_1} = 1$.

Lemma 3.2. *if* $\dfrac{m_i K_i}{a_i + K_i} - d_i < 0$, *then* $\lim_{t\to\infty} x_i(t) = 0$.

Proof.

$$\begin{aligned}\frac{x_i'(t)}{x_i(t)} &= \frac{m_i S(t)}{a_i + S(t)} - d_i \\ &\le \frac{m_i(K+\varepsilon)}{a_i + (K+\varepsilon)} - d_i = \delta_\varepsilon < 0, \ t \ge t_\varepsilon.\end{aligned}$$

if $\varepsilon > 0$ is sufficient small. Then $x_i(t) \le x(t_\varepsilon)e^{-\delta_\varepsilon(t-t_\varepsilon)} \to 0$ as $t \to \infty$. □

Remark: $\dfrac{m_i K_i}{a_i + K_i} - d_i < 0 \Leftrightarrow$ either $m_i \le d_i$ or $m_i > d_i$, and $K < \lambda_i = \dfrac{a_i}{(\frac{m_i}{d_i}) - 1} > 0$.

Theorem 3.3. *if (i)* $b_1 = \frac{m_1}{d_1} \le 1$ *or* $\lambda_1 > K$, *(ii)* $b_2 = \frac{m_2}{d_2} \le 1$ *or* $\lambda_2 > K$. *Then* $\lim_{t\to\infty} x_1(t) = \lim_{t\to\infty} x_2(t) = 0$, $\lim_{t\to\infty} S(t) = K$.

Theorem 3.4. *if (i)* $0 < \lambda_1 < K$ *and* $\lambda_2 > K$ *or* $b_2 \le 1$. *If* $\frac{K-a_1}{2} < \lambda_1$, *then* $\lim_{t\to\infty} S(t) = S^* = \lambda_1$, $\lim_{t\to\infty} x_1(t) = x_1^* = \frac{r}{m}(1-\frac{S^*}{K})(a_1+S^*) > 0$, $\lim_{t\to\infty} x_2(t) = 0$. *If* $\frac{K-a}{2} > \lambda_1$, *then the trajectory of* $(S(t), x_1(t), x_2(t))$ *approaches* $S - x_1$ *plane to a unique limit cycle* γ_1 *except a distinguished orbit (i.e. stable manifold* Γ_1 *of* $(S^*, x_1^*, 0)$*), which approaches* $(S^*, x_1^*, 0)$.*(See Fig. 34)*

Theorem 3.5. *We assume that* $0 < \lambda_1 < \lambda_2 < K$, $b_1 \ge b_2$, *then we have the same conclusion,i.e.* $x_2(t) \to 0$ *as* $t \to \infty$.

Proof. Choose $\xi > 0$, such that

$$\begin{aligned}\xi\frac{x_2'(t)}{x_2(t)} - \frac{x_1'(t)}{x_1(t)} &= \xi(m_2 - d_2)\frac{S-\lambda_2}{a_2+S} - (m_1 - d_1)\frac{S-\lambda_1}{a_1+S} \\ &= (m_1 - d_1)[\xi(\frac{m_2-d_2}{m_1-d_1})\frac{S-\lambda_2}{a_2+S} - \frac{S-\lambda_1}{a+S}] \\ &= (m_1-d_1)\frac{P_{\xi^*}(S)}{(a_1+S)(a_2+S)}\end{aligned}$$

$$P_\xi(S) = \xi^*(S-\lambda_2)(a_1+S) - (S-\lambda_1)(a_2+S)$$

Choose $\xi^* > 0$, such that, the discriminate $D < 0$, $P_{\xi^*}(S) < -\delta < 0, \forall\ 0 \le S \le K$ for some $\delta > 0$. Then

$$\begin{aligned}\left(\frac{x_2(t)}{x_2(0)}\right)^\xi &\le (\frac{x_1(t)}{x_2(0)})[\exp\int_0^t (m_1-d_1)\frac{P_{\xi^*}(S)}{(a_1+S)(a_2+S)}]dt \\ &\le M_1[\exp(m_1-d_1)\frac{(-\delta)t}{(a_1+K)(a_2+K)}]\end{aligned}$$

so $x_2(t) \to 0$ as $t \to \infty$. □

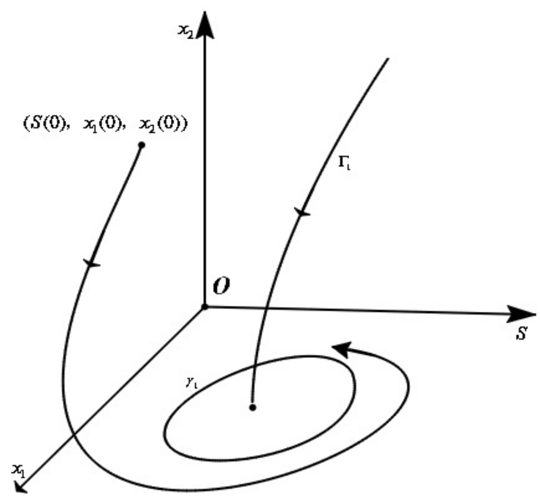

Figure 34:

Homework: Use the condition $b_1 \geq b_2$. To show the choice of $\xi^* > 0$ is possible.

Remark: Under assumption $0 < \lambda_1 < \lambda_2 < K, b_1 < b_2 \Rightarrow a_1 < a_2$.

Theorem 3.6. *if* $0 < \lambda_1 < \lambda_2 < K,\ a_1 < a_2, b_1 < b_2,\ K < \dfrac{b_1 a_2 - b_2 a_1}{b_1 - b_2}$, *then* $\lim\limits_{t\to\infty} x_2(t) = 0$.

The remaining case is $0 < \lambda_1 < \lambda_2 < K,\ a_1 < a_2,\ b_1 < b_2,\ K > \dfrac{b_1 a_2 - b_2 a_1}{b_1 - b_2}$.

First step, we want to show the existence of positive periodic solution, arising from the limit cycle in $S - x_1$ plane. (See Fig. 35 and Fig. 36.)

Open problem: Apply Lyapunov function of Ardio-Ricciardo

$$V(S, x_1, x_2) = x_1^\theta \int_{\lambda_1}^{S} \frac{\xi - \lambda_1}{\xi} + \int_{x_1^*}^{x_1} \eta^{\theta-1}(\eta - x_1^*) d\eta + c x_2.$$

To obtain GAS of (S^*, x_1^*, x_2^*).
Liearization of periodic solution $(S^*(t), x_1^*(t), 0), 0 \leq t \leq T$.

$$y' = D_x f(S^*(t), x_1^*(t), 0) y$$

$$B(t) = D_x f(S^*(t), x_1^*(t), 0) = \begin{pmatrix} A(t) & \begin{pmatrix} b_1(t) \\ b_2(t) \end{pmatrix} \\ \begin{pmatrix} 0 & 0 \end{pmatrix} & b_3(t) \end{pmatrix}$$

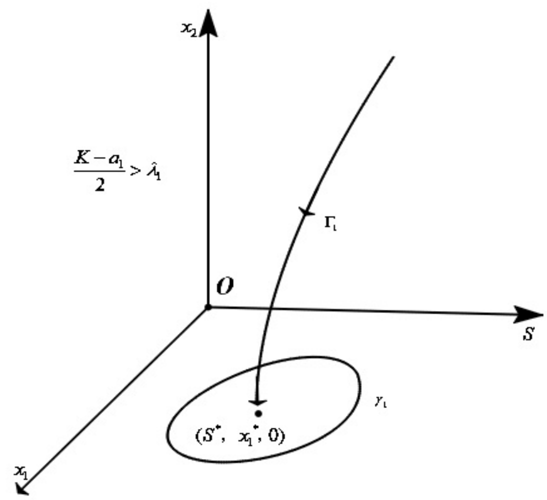

Figure 35:

$$b_3(t) = (\frac{m_2 S^*(t)}{a_2 + S^*(t)} - d_2)$$

Prove the following Lemma 3.7 as a homework.

Lemma 3.7. *Let $A(t)$ be 2×2 periodic matrix of period T. $Y(t)$ is the fundamental matrix of $y' = A(t)y, Y(0) = I$. Let $B(t)$ be 3×3 periodic matrix of period T. Then the fundamental matrix $\Phi(t)$ of $z' = B(t)z$ is given by*

$$\Phi(t) = \begin{pmatrix} Y(t) & \begin{pmatrix} z_1(t) \\ z_2(t) \end{pmatrix} \\ \begin{pmatrix} 0 & 0 \end{pmatrix} & z_3(t) \end{pmatrix} \tag{3.1}$$

$z_3(t) = exp(\int_0^t b_3(s)ds)$.

If $\rho_1 = 1,\ \rho_2 < 1$ are Floquet multipliers of $A(t)$. i.e.(eigenvalue of $Y(T)$), then the Floquet multipliers of 3×3 matrix $B(t)$, is $\rho_1,\ \rho_2, \rho_3 = z(T)$. (See Fig. 37.)

If $\rho_3 = z_3(t) < 1$, then γ_1 is orbitally stable. Hence $\int_0^T (\frac{m_2 S^*(t)}{a_2 + S^*(t)} - d_2)dt < 0$ implies γ_1 is orbitally stable.

Existence of positive periodic solution.

We shall obtain a positive periodic solution bifurcated from the limit cycle in $S - x_1$ plane.

State without proof:

Crandall-Rabinowitz bifurcation from simple eigenvalues.

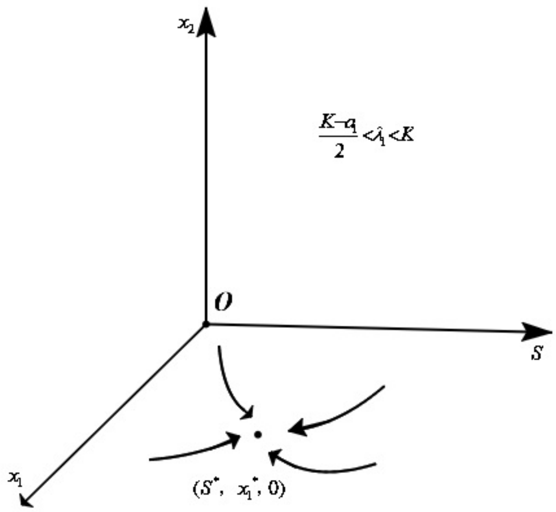

Figure 36:

Let $f : U \subseteq \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$ for $f \in C^2(U, \mathbb{R}^n)$. $f(\lambda, 0) = 0$ for all $\lambda \in \mathbb{R}$.
Let

$$L(\lambda) = D_x f(\lambda, 0)$$

$$L_0 = D_x f(\lambda_0, 0) \in \mathbb{R}^{n \times n}, \lambda_0 \text{ be the bifurcation point}$$

and

$$L_1 = D_{x\lambda} f(\lambda_0, 0) \in \mathbb{R}^{n \times n}$$

Theorem 3.8. *(Crandall-Rabinowitz)*
Assume

$$N(L_0) = span\langle u_0 \rangle,$$

$$L_1 u_0 \notin Range L_0 (Principle\ of\ exchange\ stability)$$

$$(\frac{dx}{dt} = f(\lambda, x), the\ stability\ of x = 0\ changes\ when\ \lambda = \lambda_0)$$

$$Z = \{u_0\}^{\perp},$$

Then $\exists \delta > 0$ *and* C^1*-curve* $(\lambda, \phi) : (-\delta, \delta) \to \mathbb{R} \times \mathbb{Z}, \lambda = \lambda(s), \phi = \phi(s), s \in (-\delta, \delta)$.
s.t.

(i) $\lambda(0) = \lambda_0$.

(ii) $\phi(0) = 0$.

(iii) $f(\lambda(s), s(u_0 + \phi(s)) = 0)$ *for* $|s| < \delta$.

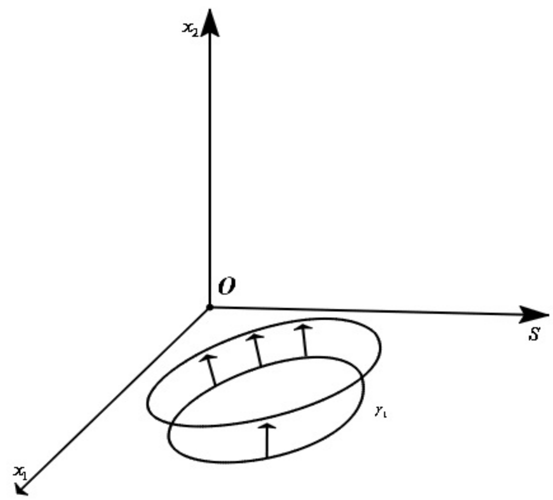

Figure 37:

Furthermore, ∃ neighborhood of $(\lambda_0, 0)$ *s.t. the zeros of f either lies on this curve or is of the form*$(\lambda, 0)$. *(See Fig. 38.)*

Proof. Let

$$\mu(a_2) = \frac{m_2}{T} \int_0^T \frac{S^*(t)}{a_2 + S^*(t)} dt$$

$$\mu(0) = m_2 > d_2$$

$$\mu(a_2) \searrow \ in\ a_2$$

$$\mu(a_2) \leq \frac{m_2}{a_2 T} \int_0^T S^*(t) dt$$

$$\mu(a_2) \to 0 \ as\ a_2 \to \infty$$

$$\exists a_2^*, s.t. \mu(a_2^*) = d_2$$

Use (Y, Z) coordinate

$$Y = x_1 - x_1(t_0)$$

$$Z = x_2$$

$$P_0 = (0, 0)$$

Consider Poincare map $P = P(Y, Z, a_2) = (P_1(Y, Z, a_2), P_2(Y, Z, a_2))$, P_0 is a fixed point of Poincare map for any a_2. See Fig. 39.

Apply Crandall-Rabinowitz theorem to P with $\lambda = a_2, \lambda_0 = a_2^*$.

$$P(0, 0, a_2) \equiv 0, \forall a_2.$$

□

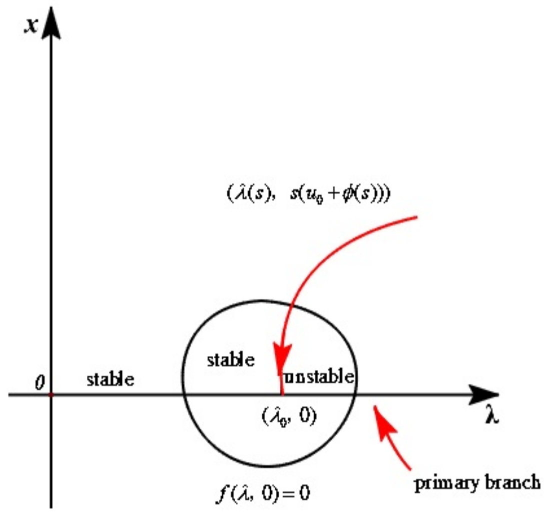

Figure 38:

Consider the equation

$$\begin{cases} S'(t) = rS(1-\dfrac{S}{K}) - \dfrac{1}{y_1}\dfrac{m_1 S}{a_1+S}x_1 - \dfrac{1}{y_2}\dfrac{m_2 S}{a_2+S}x_2 \\ x_1' = (\dfrac{m_1 S}{a_1+S} - d_1)x_1, \\ x_2' = (\dfrac{m_2 S}{a_2+S} - d_2)x_2, \end{cases}$$

Let $\frac{1}{y_1} = \frac{1}{y_2} = 1$.

Assume $0 < \lambda_1 < \lambda_2 < K$, $\lambda_i = \dfrac{a_i}{(\frac{m_i}{d_i}) - 1} > 0$. λ_i=break-even concentration. We have shown that if $b_1 \geq b_2,\ b_i = \frac{m_i}{d_i}$, then $x_2(t) \to 0$ as $t \to \infty$. Since $0 < \lambda_1 < \lambda_2,\ b_1 < b_2$, we can obtain that $a_1 < a_2$.

Consider the case if $0 < \lambda_1 < \lambda_2 < K,\ a_1 < a_2,\ b_1 < b_2,\ K < \dfrac{b_1 a_2 - b_2 a_1}{b_1 - b_2}$, then $\lim\limits_{t\to\infty} x_2(t) = 0$. Hence we consider the remaining case $0 < \lambda_1 < \lambda_2 < K,\ a_1 < a_2,\ b_1 < b_2,\ K > \dfrac{b_1 a_2 - b_2 a_1}{b_1 - b_2}$.

Existence of positive solution

Consider $\frac{K-a_1}{2} > \lambda_1$, limit cycle $\Gamma_1 = (S_1^*(t), x_1^*(t), 0)$ exists and is unique in $S - x_1$ plane. (See Fig. 40)

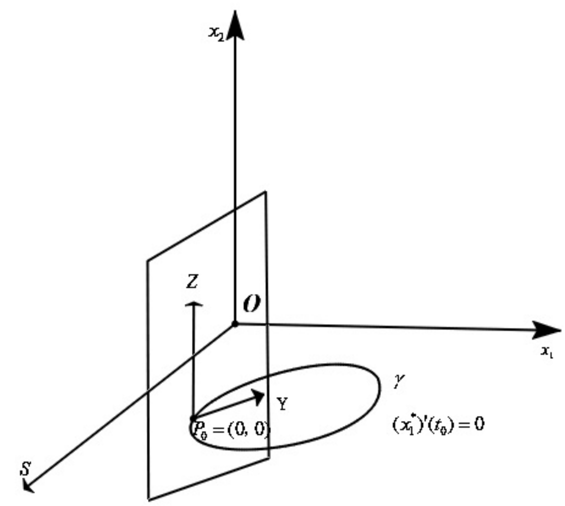

Figure 39:

Consider bifurcation from Γ_1, construct Poincare map: $\Omega \xrightarrow{P} \Omega$.

$$Y = x_1(t) - x_1(t_0)$$

$$Z = x_2(t)$$

Take a_2 as bifurcation parameter

$$P(Y, Z, a_2) = (P_1(Y, Z, a_2), P_2(Y, Z, a_2))$$

$$P(0, 0, a_2) = (0, 0),\ \forall a_2\ ((0, 0) is\ a\ fixed\ point,\ or\ \gamma\ is\ a\ periodic\ orbit)$$

$$P_2(Y, 0, a_2) = 0,\ \ \forall a_2 \text{ (since } S - x_1 \text{ plane is variant.)}$$

Define

$$\lambda = a_2,\ \ X = \begin{pmatrix} Y \\ Z \end{pmatrix}.$$

$$f(\lambda, X) = P(X, \lambda) - X$$

$$f(\lambda, \vec{0}) = \vec{0} \text{ for all } \lambda = a_2.$$

To obtain the existence of positive solution, we shall apply Crandall-Rabinowitz bifurcation Theorem from Simple eigenvalues.

Theorem 3.9. *(Crandall-Rabinowitz theorem) Let $f : U \subseteq \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}^n$ for $f \in C^2(U, \mathbb{R}^n)$. $f(\lambda, 0) = 0$ for all $\lambda \in \mathbb{R}$.*

Let

$$L(\lambda) = D_x f(\lambda, 0)$$

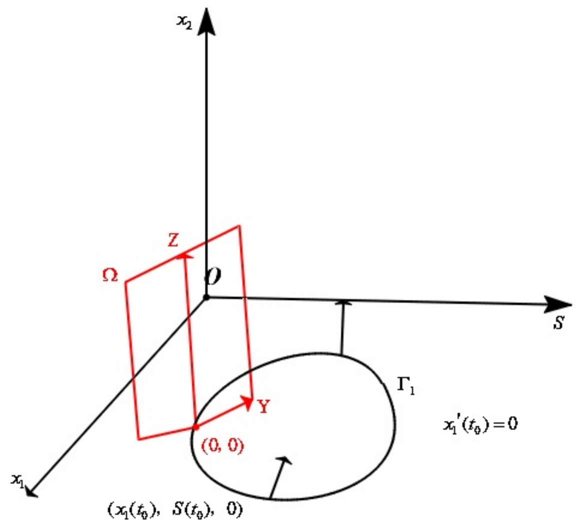

Figure 40:

$$L_0 = L(\lambda_0), L_1(\lambda) = D_\lambda L(\lambda) = L'(\lambda)$$

Let $L_1 = L_1(\lambda_0)$, λ_0 is the bifurcation point satisfies

$$N(L_0) = null\ space\ of\ L_0 = span\langle u_0 \rangle,$$

and

$$Z = \{u_0\}^\perp,$$

$L_1 u_0 \notin Range L_0 \Leftrightarrow$ Principle of exchange stability $\Leftrightarrow a'(\lambda_0) \neq 0$ ***(Homework)***

Then $\exists \delta > 0$ and C^1-curve $(\lambda, \phi) : (-\delta, \delta) \to \mathbb{R} \times \mathbb{Z}, \lambda = \lambda(s), \phi = \phi(s), s \in (-\delta, \delta)$. such that

(i) $\lambda(0) = \lambda_0$.

(ii) $\phi(0) = 0$.

(iii) $f(\lambda(s), s(u_0 + \phi(s)) = 0)$ *for* $|s| < \delta$.*(See Fig. 41)*

Consider

$$\frac{dx}{dt} = f(\lambda, x)$$

Consider Linearization at $x = 0$

$$\frac{dy}{dt} = D_x f(\lambda, 0) y = L(\lambda) y.$$

Let

$$y(t) = e^{a(\lambda)t}\psi(\lambda) \ \Rightarrow\ a(\lambda)\psi(\lambda) = L(\lambda)\psi(\lambda)$$

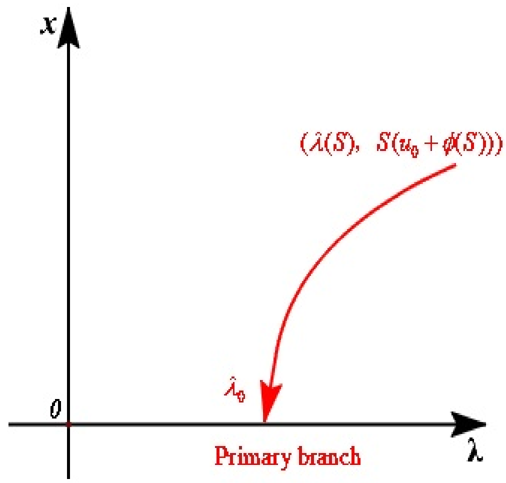

Figure 41:

$$L(\lambda_0) = L_0,\ a(\lambda_0) = 0,\ \psi(\lambda_0) = u_0.$$
$$L_1 u_0 \notin Range L_0 \Leftrightarrow a'(\lambda_0) \neq 0.$$

Remark on ODE([H], P. 105):

Floquet multipliers of $(S^*(t), x_1^*(t), 0)$ *are exactly the eigenvalues of* $D_x P(0,0)$.

Floquet multipliers of $(S_1^*(t), x_1^*(t), 0)$ are eigenvalues of Fundamental matrix $\Phi(T),\ \Phi(0) = I$ of $y' = J(S^*(t), x_1^*(t), 0)y$, they are 1, ρ_1 *and* ρ_2, $\rho_1 < 1$(since limit cycle γ_1 in the $S - x_1$ plane is orbitally stable unique). $\rho_2(a_2) = \rho_2 = \exp(\int_0^T \frac{m_2 S^*(t)}{a_2+S^*(t)} - d_1)$

Since

$$D_x P(0,0,a_2) = \begin{pmatrix} \dfrac{\partial P_1}{\partial Y}(0,0,a_2) & \dfrac{\partial P_1}{\partial Z}(0,0,a_2) \\ \dfrac{\partial P_2}{\partial Y}(0,0,a_2) & \dfrac{\partial P_2}{\partial Z}(0,0,a_2) \end{pmatrix} = \begin{pmatrix} \dfrac{\partial P_1}{\partial Y}(0,0,a_2) & \dfrac{\partial P_1}{\partial Z}(0,0,a_2) \\ 0 & \dfrac{\partial P_2}{\partial Z}(0,0,a_2) \end{pmatrix}.$$

Hence $\frac{\partial P_1}{\partial Y}(0,0,a_2) = \rho_1 < 1$ and $\frac{\partial P_2}{\partial Z}(0,0,a_2) = \rho_2$.

Let $\lambda_0 = a_2^*$ satisfies

$$\int_0^T \frac{m_2 S^*(t)}{a_2^* + S^*(t)} - d_1 = 0$$

then $\rho_2(a_2^*) = 1$.

Let

$$L(\lambda) = D_x f(\lambda, 0) = D_x P(0, a_2) - I$$

$$u_0 = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}.$$

$$L(\lambda_0)\begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} \rho_1 - 1 & \frac{\partial P_1}{\partial Z}(0,0,a^*) \\ 0 & \rho_2(a_2^*) - 1 \end{pmatrix}\begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

we obtain

$$(\rho_1 - 1)v_1 + \frac{\partial P_1}{\partial Z}(0,0,a_2^*)v_2 = 0.$$

Take

$$\overrightarrow{u_0} = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} \frac{\partial P_1}{\partial Z}(0,0,a_2^*) \\ 1 - \rho_1 \end{pmatrix}.$$

$$\rho_2'(a_2^*) \neq 0$$

Since $\rho_2(a_2) \searrow$ in a_2. By C-R Theorem and $1 - \rho_1 > 0$, there exists positive periodic solution.

Open problem: $0 < \lambda_1 < \lambda_2 < K,\ a_1 < a_2,\ b_1 < b_2,\ K > \dfrac{b_1 a_2 - b_2 a_1}{b_1 - b_2}$. Since the bifurcation results are local, we have existence of positive periodic solution, where $|a_2 - a_2^*| < \delta$. Prove the global results shown in Fig. 42.

Ecological Monograph (1978)

$$\begin{array}{lll} r = 20\ln 2 & a_2 = 720 & \\ d_1 = \frac{\ln 2}{2} & m_1 = \ln 2 & i.e.\ b_1 = 2 \\ d_2 = \ln 2 & m_2 = 4\ln 2 & \quad b_2 = 4 \\ \gamma_1 = 0.1 & & \end{array}$$

See Fig. 42 and Fig. 43.

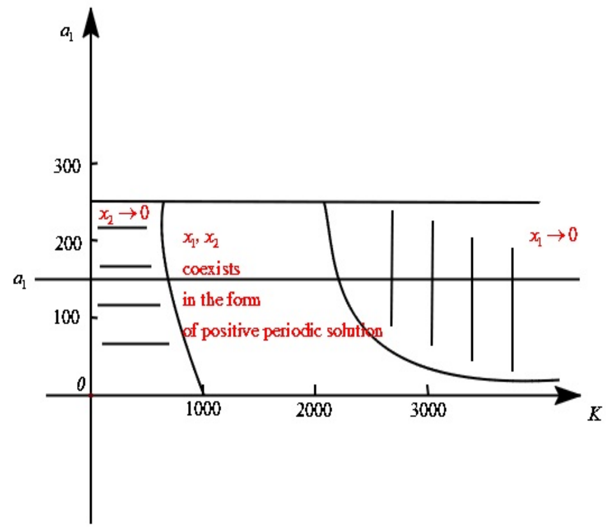

Figure 42:

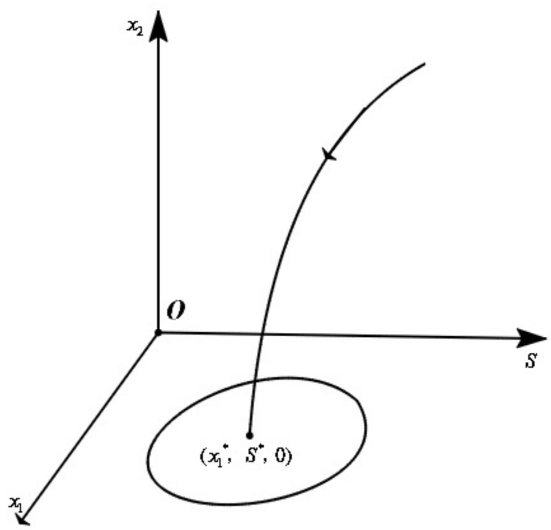

Figure 43:

4 Lecture 4 Two Species Competing for Two Complementary Resource and Two Substitutable Resources in a Chemostat

Consider two species compete for two complementary resources S and R. (e.g. nitrogen and phosphors) in a chemostat. The equations are:

$$\begin{cases} S' = (S^{(0)} - S)D - \frac{1}{y_{s1}} g_1(S,R)x_1 - \frac{1}{y_{s2}} g_2(S,R)x_2 \\ R' = (R^{(0)} - R)D - \frac{1}{y_{r1}} g_1(S,R)x_1 - \frac{1}{y_{r2}} g_2(S,R)x_2 \\ x_1' = (g_1(S,R) - D)x_1 \\ x_2' = (g_2(S,R) - D)x_2 \end{cases} \quad (1)$$

$$g_1(S,R) = min(\frac{m_{s1}S}{a_{s1}+S}, \frac{m_{r1}R}{a_{r1}+R})$$

$$g_2(S,R) = min(\frac{m_{s2}S}{a_{s2}+S}, \frac{m_{r2}R}{a_{r2}+R})$$

Lieberg's Law of minimum.

Analysis: $S' + \frac{1}{y_{s1}}x_1' + \frac{1}{y_{s2}}x_2' = S^{(0)} + D(S + \frac{1}{y_{s1}}x_1 + \frac{1}{y_{s2}}x_2)$.
Conservation Law:

$$S(t) + \frac{1}{y_{s1}}x_1(t) + \frac{1}{y_{s2}}x_2(t) = S^{(0)} + O(e^{-Dt})$$

Similarly we have

$$R(t) + \frac{1}{y_{r1}}x_1(t) + \frac{1}{y_{r2}}x_2(t) = R^{(0)} + O(e^{-Dt})$$

Consider the limiting equations:

$$\begin{cases} x_1' = [g_1(S^{(0)} - \frac{1}{y_{s1}}x_1 - \frac{1}{y_{s2}}x_2, R^{(0)} - \frac{1}{y_{r1}}x_1 - \frac{1}{y_{r2}}x_2) - D]x_1 \\ x_2' = [g_2(S^{(0)} - \frac{1}{y_{s1}}x_1 - \frac{1}{y_{s2}}x_2, R^{(0)} - \frac{1}{y_{r1}}x_1 - \frac{1}{y_{r2}}x_2) - D]x_2 \end{cases} \quad (2)$$

We reduce the system of 4 equations to a competitive system of 2 equations.
The isolines of (1) take forms like Fig. 44 and Fig. 45.

Remark: The limiting system (2) and original system (1) have the same solution behavior. We can find the proofs in [SW] (Appendix F, A Convergence Theorem) and in [Z1](P. 17)

From Fig. 46. We can see species 1 is better competitor w.r.t. S and R. $\because \lambda_{s1} < \lambda_{s2}, \lambda_{r1} < \lambda_{r2}, \therefore$ species 1 win.
From Fig. 37 . We can see species 2 is a better competitor for S, species 1 is a better competitor for R.

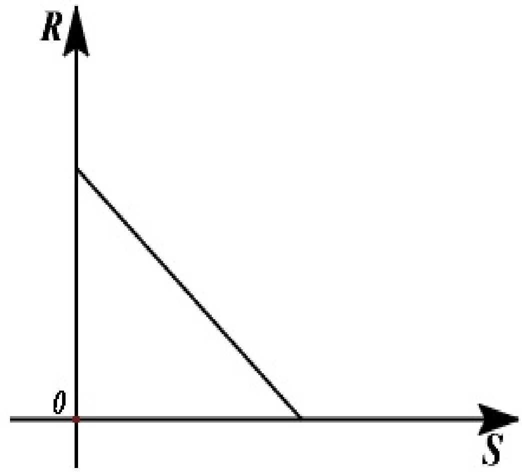

Figure 44:

Species 1 is S-limited if species 1 is R-limited if Species 2 is S-limited if species 2 is R-limited if

$$T_1 = \frac{(R^{(0)} - \lambda_{r1})}{(S^{(0)} - \lambda_{s1})}$$

T_1 be the ratio of steady state nutrient regeneration rate of equilibrium.

Definition: We say species 1 is S-limited if $T_1 > C_1 = \frac{y_{s1}}{y_{r1}}$.

Definition: We say species 1 is R-limited if $T_1 < C_1 = \frac{y_{s1}}{y_{r1}}$.

$$T_2 = \frac{(R^{(0)} - \lambda_{r2})}{(S^{(0)} - \lambda_{s2})}$$

Definition: We say species 2 is S-limited if $T_2 > C_2 = \frac{y_{s2}}{y_{r2}}$.

Definition: We say species 2 is R-limited if $T_2 < C_2 = \frac{y_{s2}}{y_{r2}}$.

$$\lambda_{si} = \frac{a_{si}}{(\frac{m_{si}}{D}) - 1}, i = 1, 2.$$

$$\lambda_{ri} = \frac{a_{ri}}{(\frac{m_{ri}}{D}) - 1}, i = 1, 2.$$

$$C_i = \frac{y_{si}}{y_{ri}}, i = 1, 2.$$

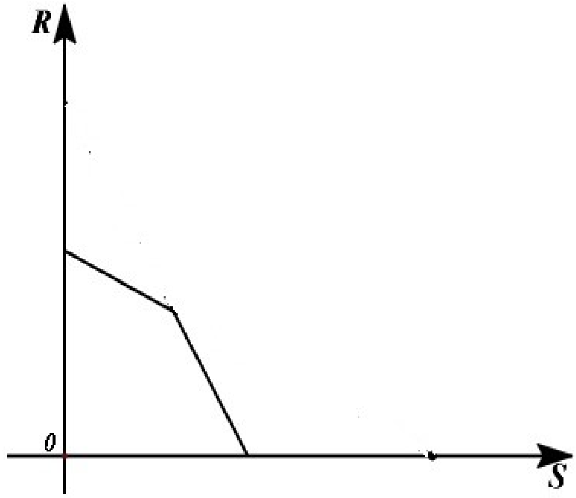

Figure 45:

Assume

(H_1) $0 < \lambda_{s1} < \lambda_{s2} < S^{(0)}, 0 < \lambda_{r1} < \lambda_{r2} < R^{(0)}$.

From Fig. 48. Species 1 has lower break-even concentration with respect to both S and R. Hence we predict species 1 wins, species 2 lose.

From Fig. 49. $E_{s1} = (\lambda_{s1}, R^*_{s1}, x^*_{s1}, 0), R^*_{s1} > \lambda_{r1}$, species 1 wins.

Either E_{s1} or E_{r1} exists according to species 1 is S-limited or R-limited.

$$\lim_{t\to\infty}(S(t), R(t), x_1(t), x_2(t)) = E_{s1}.$$

$$\lim_{t\to\infty}(S(t), R(t), x_1(t), x_2(t)) = E_{r1}.$$

(H_2) $\lambda_{r1} < \lambda_{r2}, \lambda_{s2} < \lambda_{s1}$.

Define
$$T^* = \frac{R^{(0)} - \lambda_{r2}}{S^{(0)} - \lambda_{s1}}$$

There are four cases.

Case 1: $T^* < C_1, C_2$.

Then $T_2 < T^* < C_2$. $\therefore x_2$ is R-limited. But species 1 has lower break-even concentration with respect to resource R, *i.e.*, $\lambda_{r1} < \lambda_{r2}$. Biologically we predict x_2 loses competition and x_1 wins. Then $(S(t), R(t), x_1(t), x_2(t)) \to E_{s1}$ if x_1 is S-limited. $(S(t), R(t), x_1(t), x_2(t)) \to E_{r1}$ if x_1 is R-limited.

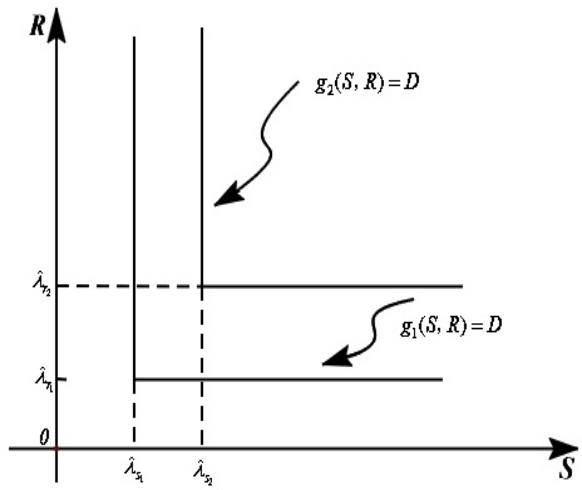

Figure 46:

Case 2: $T^* > C_1, C_2$.

Then $T_1 > T^* > C_1$. $\therefore$ x_1 is S-limited. But species 2 has lower lower break-even concentration with respect to resource S, *i.e.*, $\lambda_{s2} < \lambda_{s1}$. Then we predict that x_2 win the competition. Then $(S(t), R(t), x_1(t), x_2(t)) \to E_{s2}$ if x_2 is S-limited. $(S(t), R(t), x_1(t), x_2(t)) \to E_{r2}$ if x_2 is R-limited.

Case 3: $C_1 < T^* < C_2$.

Then $T_2 < T^* < C_2$. $\therefore$ x_2 is R-limited. $C_1 < T^* < T_1$. $\therefore$ x_1 is S-limited.

$\because$ species 2 has lower $\lambda_{s2} < \lambda_{s1}$. species 1 has lower $\lambda_{r1} < \lambda_{r2}$.

$\therefore E_c = (\lambda_{s1}, \lambda_{r2}, x_{1c}^*, x_{2c}^*)$ exists and is GAS.

Case 4: $C_2 < T^* < C_1$.

E_c is unstable.

(a) x_1 is S-limited, x_2 is S-limited. $(E_{s1}), (E_{s2})$ are LAS.

(b) x_1 is S-limited, x_2 is R-limited. $(E_{s1}), (E_{r2})$ are LAS.

(c) x_1 is R-limited, x_2 is S-limited. $(E_{r1}), (E_{s2})$ are LAS.

(d) x_1 is R-limited, x_2 is R-limited. $(E_{r1}), (E_{r2})$ are LAS.

Tilmman's graph:
$C_2 < T^* < C_1$. See Fig. 50.
$C_1 < T^* < C_2$. See Fig. 51.
Open problem:

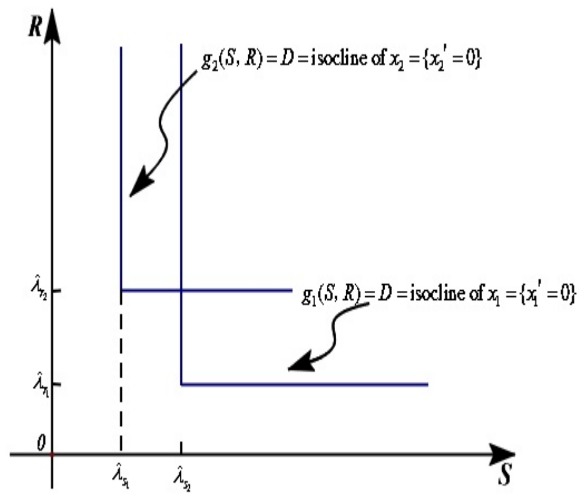

Figure 47:

$$\text{If} \begin{cases} x_1' = (g_1(S,R) - d_1)x_1 \\ x_2' = (g_2(S,R) - d_2)x_2 \\ d_1, d_2 \neq D \end{cases}$$

$$\lambda_{si} = \frac{a_{si}}{(\frac{m_{si}}{d_i}) - 1}, \lambda_{ri} = \frac{a_{ri}}{(\frac{m_{ri}}{d_i}) - 1}.$$

Then there are no conservation laws. Prove same results holds as the case $d_1 = d_2 = D$.

Open problem:

Consider n-species compete for two complementary resources with same D. Prove there are at most 2 species survives, i.e. competitive exclusion principle holds.(SIAP,2001,B.Li and Hal Smith.)

Open problem:

Jef Huisman consider n-species compete for m complementary resources. For the case $n = 9, m = 3$, 9 species coexist in the periodic solution form 3 complementary resources.(Nature, 2000)

Two species compete for two substitutable resources S and R.

$$\begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - \frac{1}{y_{s1}} \frac{\frac{m_{s1}}{a_{s1}} S}{1 + \frac{S}{a_{s1}} + \frac{R}{a_{r1}}} x_1 - \frac{1}{y_{s2}} \frac{\frac{m_{r1}}{a_{r1}} R}{1 + \frac{S}{a_{s1}} + \frac{R}{a_{r1}}} x_2 \\ \frac{dR}{dt} = (R^{(0)} - R)D - \frac{1}{y_{s2}} \frac{\frac{m_{s2}}{a_{s2}} S}{1 + \frac{S}{a_{s2}} + \frac{R}{a_{r2}}} x_1 - \frac{1}{y_{r2}} \frac{\frac{m_{r2}}{a_{r2}} R}{1 + \frac{S}{a_{s2}} + \frac{R}{a_{r2}}} x_2 \\ \frac{dx_1}{dt} = x_1 (\frac{\frac{m_{s1}}{a_{s1}} S + \frac{m_{r1}}{a_{r1}} R}{1 + \frac{S}{a_{s1}} + \frac{R}{a_{r1}}} - D) x_1 \\ \frac{dx_1}{dt} = x_2 (\frac{\frac{m_{s2}}{a_{s2}} S + \frac{m_{r2}}{a_{r2}} R}{1 + \frac{S}{a_{s2}} + \frac{R}{a_{r2}}} - D) x_2 \end{cases}$$

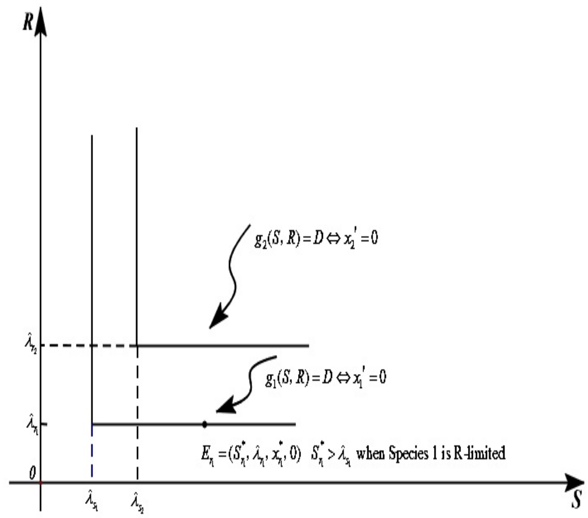

Figure 48:

We note that if $R = 0$, then $x_1' = (\frac{m_{s1}S}{a_{s1}+S} - D)x_1$, if $S = 0$, then $x_1' = (\frac{m_{r1}R}{a_{r1}+R} - D)x_1$

Write

$$x_1' = x_1 D(\frac{\frac{S}{\lambda_{s1}} + \frac{R}{\lambda_{r1}} - 1}{1 + \frac{S}{a_{s1}} + \frac{R}{a_{r1}}})$$

$$x_2' = x_2 D(\frac{\frac{S}{\lambda_{s2}} + \frac{R}{\lambda_{r2}} - 1}{1 + \frac{S}{a_{s2}} + \frac{R}{a_{r2}}})$$

From Fig. 53. Species 1 has lower break-even concentrations λ_{s1} and λ_{r1} w.r.t. both resource S and R. We predict that species 1 wins biologically. However it is difficult to give a rigorous mathematical proof.

We note that the system has no conservation law even with same D.

Open problem:

Analyse the system's global behavior. (Local analysis was already done in [WHH].)

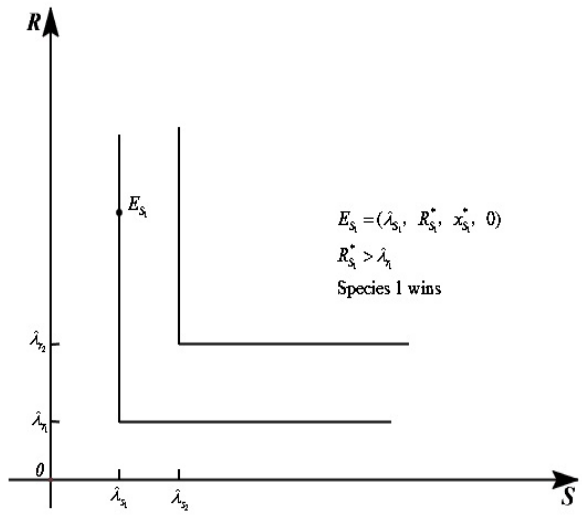

Figure 49:

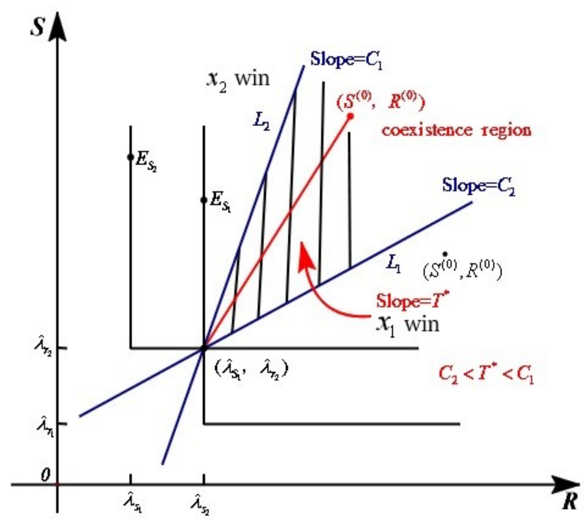

Figure 50:

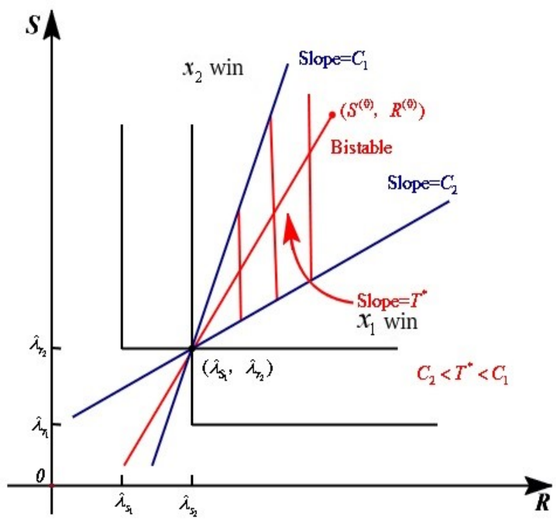

Figure 51:

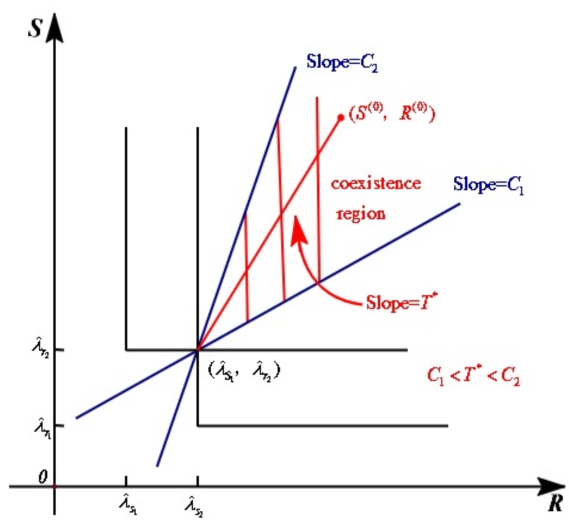

Figure 52:

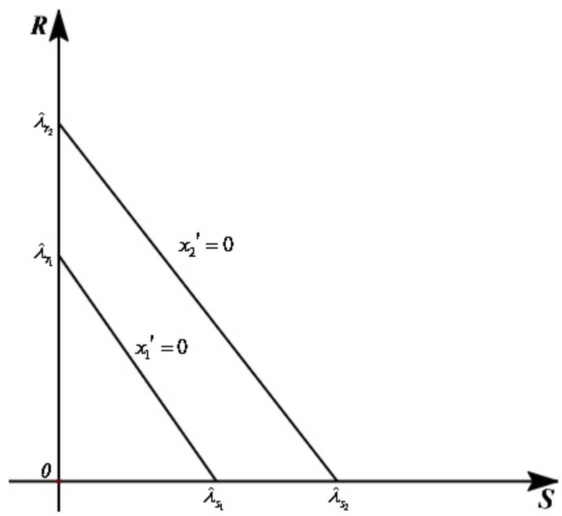
R
$\hat{\lambda}_{r_2}$
$\hat{\lambda}_{r_1}$
$x_2' = 0$
$x_1' = 0$
0
$\hat{\lambda}_{s_1}$
$\hat{\lambda}_{s_2}$
S

Figure 53:

5 Lecture 5 Monotone Dynamical System[S] with applications to simple chemostat equations with inhibition[HW] and May-Leonard model of three competing species[CHW]

Dynamics are divided into two cases: Chaotic-dynamics and Regular-dynamics.

Regular-dynamics: Solution tends to equilibrium points or solution approaches limit cycle. To deal with these cases, we usually use the following methods:

(i) Constructing Lyapunov functions.

(ii) When $n = 2$, use Poincare-Bendixsm Theorem to prove global stability of LAS equilibrium and uniqueness of limit cycles.

(iii) When $n \geq 3$, Hopf Bifurcation indicates the possibility of occurrence of periodic solution at some bifurcation points.

Consider O.D.E.:

$$x' = f(x),\ f:\ D \subseteq \mathbb{R}^n \to \mathbb{R}^n$$

$$f = (f_1 ... f_n),\quad x = (x_1 ... x_n)$$

We generalize scalar differential inequalities to system.

Definition: $a \leq b \Leftrightarrow a_i \leq b_i,\quad i = 1, 2, ..., n.$

Theorem 5.1. *(Kamke's Theorem) Let $x' = f(x)$ be a cooperative system i.e. $\frac{\partial f_i}{\partial x_j}(x) \geq 0,\ i \neq j$. If $x(t)$ satisfies*

$$\begin{cases} x' \leq f(x) \\ x(0) \leq x_0. \end{cases}$$

and $\varphi(t)$ satisfies

$$\begin{cases} \varphi' = f(\varphi) \\ \varphi(0) = x_0. \end{cases}$$

Then $x(t) \leq \varphi(t),\ t \geq 0$.

Consider two solutions φ, ψ of $x' = f(x)$, $\varphi(0) \leq \psi(0)$, then $\varphi(t) \leq \psi(t)$ for all $t \geq 0$. Let $\Phi(t, x_0)$ be the solution $x(t, x_0)$ of

$$\begin{cases} x' = f(x) \\ x(0) = x_0. \end{cases}$$

Write

$$\Phi_t(x_0) = \Phi(t, x_0)$$

Definition: We say that $\Phi_t(x)$ is a monotone flow, if $x \leq y$, then $\Phi_t(x) \leq \Phi_t(y),\ \forall\ t > 0$.

Definition: We say that $\Phi_t(x)$ is a strong monotone flow, if $x \le y$, then $\Phi_t(x) \ll \Phi_t(y),\ \forall t > 0$. Here $a \ll b \Leftrightarrow a_i < b_i,\ \forall i = 1, 2, ..., n$

(Hirsch): A cooperative system $x' = f(x)$ generates a strong monotone flow, provided $D_x f(x)$ is an $n \times n$ irreducible matrix. $\forall x \in D$.

Definition: A matrix is irreducible if it is not reducible. A matrix M is reducible if it is of the form

$$\begin{bmatrix} A & B \\ 0 & C \end{bmatrix}$$

under permutation.

(Hirsch): For almost all initial point x, we have $\Phi_t(x) \to e \in E$ =set of equilibrium points.

(Hirsch): Every periodic solution is unstable.

(Hirsch's Convergence Theorem): Let $\Phi_t(x)$ be bounded for $t \ge 0$, if $\exists\, T > 0$, $\exists\, x \in D$, such that $x \le \Phi_T(x)$ or $\Phi_T(x) \le x$, then $\Phi_t(x) \to e \in E$ as $t \to \infty$.

(Hirsch): No two points are ordered in the ω-limit set $w(x)$.

(i)Consider a competition system of two equations:

$$\begin{cases} x_1' = f_1(x_1, x_2) \\ x_2' = f_2(x_1, x_2) \\ \frac{\partial f_1}{\partial x_2} \le 0, \quad \frac{\partial f_2}{\partial x_1} \le 0. \end{cases}$$

Under the change variables $(x_1, x_2) \to (y_1, y_2)$, $y_1 = x_1,\ y_2 = -x_2$, we obtain that

$$\begin{cases} y_1' = g_1(y_1, y_2) \\ y_2' = g_2(y_1, y_2) \\ \dfrac{\partial g_1}{\partial y_2} = \dfrac{\partial f_1}{\partial x_2}(-1) \ge 0 \\ \dfrac{\partial g_2}{\partial y_1} = -\dfrac{\partial f_2}{\partial x_1}(y_1, -y_2) \ge 0 \end{cases}$$

is a cooperative system.

(ii)(Hirsch) Let $x' = f(x),\ x \in \mathbb{R}^3,\quad f : D \subseteq \mathbb{R}^3 \to \mathbb{R}^3$, be a 3-dim. competitive system $x' = f(x)$, *i.e.* $\frac{\partial f_i}{\partial x_j} \le 0,\ i \ne j$. If $\varphi(t)$ be a bounded solution, then Poincare-Bendixosm Theorem holds, i.e., $w(\varphi(0))$, the w-limit set, is a periodic orbit if $w(\varphi(0))$ does not contain equilibrium points.

Theorem 5.2. *(Differential Inequalities for Two Species Competition system)*[SW]

$$x'(t) = f(x), \ \frac{\partial f_1}{\partial x_2} \le 0, \ \ \frac{\partial f_2}{\partial x_1} \le 0$$

Notation: $\vec{a} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} \leq_K \vec{b} \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}$ *iff* $a_1 \leq b_1; a_2 \geq b_2$.

If $x(t)$ *satisfies* $x'(t) \leq_K f(x(t))$ *and*

$$\begin{cases} u'(t) = f(u(t)), \\ u(0) \text{ is given.} \end{cases}$$

and $x(0) \leq_K u(0)$, *then* $x(t) \leq_K u(t)$ *for* $t \geq 0$.

Simple Chemostat Equations with inhibition

Consider the equation[HW]

$$(1) \begin{cases} S'(t) = (S^{(0)} - S)D - \dfrac{1}{y_1}\dfrac{m_1 S}{a_1 + S}e^{-\eta P}x_1 - \dfrac{1}{y_2}\dfrac{m_2 S}{a_2 + S}x_2 \\ x_1'(t) = (\dfrac{m_1 S}{a_1 + S}e^{-\eta P} - D)x_1, \\ x_2'(t) = (\dfrac{m_1 S}{a_1 + S} - D)x_2, \\ P'(t) = (P^{(0)} - P)D - \dfrac{\delta P x_2}{K + P} \\ S(0) \geq 0,\ x_1(0) > 0,\ x_2(0) > 0,\ p(0) \geq 0. \end{cases}$$

where $S(t)$ is the nutrient concentration, $x_1(t), x_2(t)$ are concentration of micro-organisms. The growth of $x_1(t)$ is inhibited by antibody $P(t)$ *and* $x_2(t)$ consumes antibody.

Scaling(Nondimensional Process)

$$S \to \frac{S}{S^{(0)}}\ ,\ P \to \frac{P}{P^{(0)}}$$

$$x_1 \to x_1 \frac{1}{S^{(0)}\gamma_1}\ ,\ a_1 \to \frac{a_1}{S^{(0)}}$$

$$a_2 \to \frac{a_2}{S^{(0)}}\ ,\ x_2 \to x_2 \frac{1}{S^{(0)}\gamma_2}$$

$$t \to Dt\ ,\ m_1 \to \frac{m_1}{D}\ ,\ m_2 \to \frac{m_2}{D}$$

$$K \to \frac{K}{P^{(0)}}\ ,\ \delta \to \frac{\delta}{P^{(0)}D} y_2 S^{(0)}$$

we obtain

$$(2) \begin{cases} S' = (1 - S) - \dfrac{m_1 S}{a_1 + S}e^{-\eta P} - \dfrac{m_2 S}{a_2 + S}x_2 \\ x_1' = (\dfrac{m_1 S}{a_1 + S}e^{-\eta P} - 1)x_1, \\ x_2' = (\dfrac{m_1 S}{a_1 + S} - 1)x_2, \\ P' = (1 - P) - \dfrac{\delta P x_2}{K + P}. \end{cases}$$

Replace $e^{-\eta P}$ by $f(P)$, $f(P)$ satisfies $f(0) = 1$ and $f'(P) < 0$. (See Fig. 54)

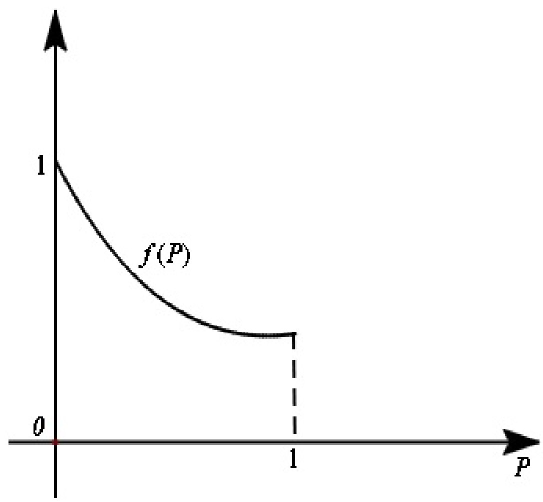

Figure 54:

Then (2) becomes

$$(3)\begin{cases} S' = (1-S) - \dfrac{m_1 S}{a_1+S} f(P) - \dfrac{m_2 S}{a_2+S} x_2 \\ x_1' = (\dfrac{m_1 S}{a_1+S} f(P) - 1) x_1, \\ x_2' = (\dfrac{m_1 S}{a_1+S} - 1) x_2, \\ P' = (1-P) - \dfrac{\delta P x_2}{K+P}. \end{cases}$$

Conservation:

$$S' + x_1' + x_2' = 1 - (S + x_1 + x_2)$$

we obtain

$$S(t) + x_1(t) + x_2(t) = 1 + O(e^{-t})$$

Consider limiting system:

$$(4)\begin{cases} x_1' = (\dfrac{m_1(1-x_1-x_2)}{a_1+(1-x_1-x_2)} f(P) - 1) x_1, \\ x_2' = (\dfrac{m_2(1-x_1-x_2)}{a_2+(1-x_1-x_2)} - 1) x_2, \\ P' = (1-P) - \dfrac{\delta P x_2}{K+P} \\ x_1(0) > 0,\ x_2(0) > 0,\ x_1(0) + x_2(0) < 1, P(0) \geq 0. \end{cases}$$

We note that system (3) and system (4) have the same solution behavior by [SW](Appendix F) and [Z1](P. 17).

Consider the important case $m_1 > 1,\ m_2 > 1$, and we have four parameters, namely $\lambda_1,\ \lambda_2,\ \lambda_+,\ \lambda_-$.

$$\frac{m_1\lambda_1}{a_1+\lambda_1} = 1, \quad \frac{m_2\lambda_2}{a_2+\lambda_2} = 1$$

$$\frac{m_1\lambda^+}{a_1+\lambda^+}f(1) = 1, \quad \frac{m_1\lambda^-}{a_1+\lambda^-}f(P^*) = 1$$

where $P^*,\ 0 < P^* < 1$ is the positive root of $(1-z)(K+z) - \delta z(1-\lambda_2) = 0$, we have $\lambda_1 < \lambda^- < \lambda^+$.(See Fig. 55)

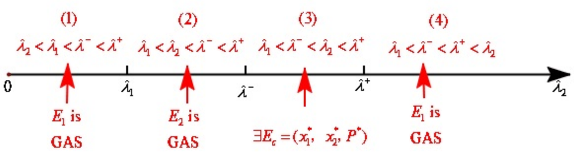

Figure 55:

We have the following three equilibria:

$$E_0 = (0,0,1) \qquad x_1 = x_2 = 0, P = 1$$

$$E_1 = (1-\lambda^+, 0, 1) \qquad x_2 = 0, P = 1, x_1 = 1-\lambda^+$$

$$E_2 = (0, 1-\lambda_2, P^*) \quad x_1 = 0, x_2 = 1-\lambda_2, P = P^*$$

E_0 is GAS, if $\lambda_1 > 1,\ \lambda_2 > 1,\ i.\ e.\ x_1 \to 0, x_2 \to 0$ as $t \to \infty$.
E_1 is GAS, if $\lambda_2 < \lambda_1 < \lambda^- < \lambda^+$.
E_2 is GAS, if $\lambda_1 < \lambda_2 < \lambda^- < \lambda^+$.
E_1 is GAS, if $\lambda_1 < \lambda^- < \lambda^+ < \lambda_2$.

If $\lambda^- < \lambda_2 < \lambda^+$, then $E_c = (x_1^*, x_2^*, P^*)$ exists,and if $\lambda_2 > 1$, we obtain $x_2 \to 0$ as $t \to \infty$.

Let $\lambda_1 > 1,\ \lambda_2 > 1$. Since $x_2(t) \to 0$, consider limiting equation, then

$$x_1' = \left(\frac{m_1(1-x_1)}{a_1+(1-x_1)}f(P) - 1\right)x_1 \le \left(\frac{m_1(1-x_1)}{a_1+(1-x_1)}f(0) - 1\right)x_1$$

we obtain $x_1 \to 0$ as $t \to \infty$, hence $P(t) \to 1$.

Theorem 5.3. *(Differential Inequality for Two Species Competition system)*

Define: $\vec{a} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} \le_K \vec{b} \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}\ iff\ a_1 \le b_1, a_2 \ge b_2.$

Let $\vec{x}(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix}$ *satisfy* $\vec{x}'(t) = \begin{pmatrix} x_1'(t) \\ x_2'(t) \end{pmatrix} \leq_K f(\vec{x}(t)) = \begin{pmatrix} f_1(x_1, x_2) \\ f_2(x_1, x_2) \end{pmatrix}$.
Let $\vec{u}(t)$ *be the solution of*

$$\begin{cases} \vec{u}'(t) = f(u(t)), \\ \vec{u}(0) \geq \vec{x}(0). \end{cases}$$

Then $\vec{x}(t) \leq_K \vec{u}(t),\ \forall\ t \geq 0.$

Theorem 5.4. *If* $0 < \lambda^+ < \lambda_2$, *then* $\lim_{t\to\infty} x_1(t) = x_1^* = 1 - \lambda^+$, $\lim_{t\to\infty} x_2(t) = 0$, $\lim_{t\to\infty} P(t) = 1$

Proof. Since $\lambda^+ = \frac{a_1}{m_1 f(1)-1} < \lambda_2$, $\exists\, \varepsilon > 0$ *small*, such that $0 < \frac{a_1}{m_1 f(1+\varepsilon)-1} < \lambda_2$. Since $P(t) < 1 + \varepsilon$ for large t, then

$$f(P(t)) > f(1+\varepsilon),$$

$$x_1' \geq (\frac{m_1(1 - x_1 - x_2)}{a_1 + (1 - x_1 - x_2)} f(1+\varepsilon) - 1)x_1,$$

$$x_2' \leq (\frac{m_2(1 - x_1 - x_2)}{a_2 + (1 - x_1 - x_2)} - 1)x_2.$$

From above differential inequalities, it follows that

$$\begin{cases} x_1(t) \geq u_1(t), \\ x_2(t) \leq u_2(t). \end{cases}$$

where $u_1(t), u_2(t)$ satisfy $u_1(0) \leq x_1(0),\ u_2(0) \geq x_2(0)$,

$$\begin{cases} u_1' = (\dfrac{m_1(1 - u_1 - u_2)}{a_1 + (1 - u_1 - u_2)} - 1)u_1, \\ u_2' = (\dfrac{m_2(1 - u_1 - u_2)}{a_2 + (1 - u_1 - u_2)} - 1)u_2. \end{cases}$$

By Fig. 56 when $\lambda^+ < \lambda_2$, *i. e.* $1 - \lambda^+ > 1 - \lambda_2$, we obtain that

$$u_1(t) \to 1 - \frac{a_1}{m_1 f(1+\varepsilon) - 1} > 0 \ as\ t \to \infty$$

$$u_2(t) \to 0$$

Since $u_2(t) \to 0$, and $x_2(t) \leq u_2(t)$ then $x_2(t) \to 0$, hence $P(t) \to 1$ and $x_1(t) \to x_1^* = 1 - \lambda^+$. □

Theorem 5.5. *If* $\lambda_1 < \lambda_2 < \lambda^-$, *then* $\lim_{t\to\infty} x_1(t) = 0$, $\lim_{t\to\infty} x_2(t) = x_2^* = 1 - \lambda_2$, $\lim_{t\to\infty} P(t) = P^*$.

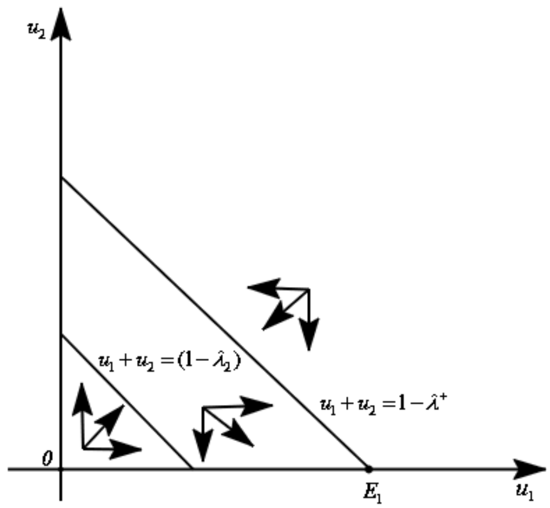

Figure 56:

Proof. Since
$$x_2' \leq (\frac{m_2(1-x_2)}{a_2+(1-x_2)} - 1)x_2,$$
we obtain
$$x_2(t) \leq 1 - \lambda_2 + \varepsilon, \quad \forall t \geq t_\varepsilon.$$
Since
$$P' \geq 1 - P - \frac{\delta P(1-\lambda_2+\varepsilon)}{K+P},$$
we obtain
$$P(t) \geq P^* + \varepsilon,$$
$$x_1' \leq (\frac{m_1(1-x_1-x_2)}{a_1+(1-x_1-x_2)} f(P^*+\varepsilon) - 1)x_1 \leq (\frac{m_1(1-x_1)}{a_1+(1-x_1)} f(P^*+\varepsilon) - 1)x_1,$$
$$x_2' = (\frac{m_2(1-x_1-x_2)}{a_2+(1-x_1-x_2)} - 1)x_2.$$
if $m_1 f(P^*+\varepsilon) \leq 1$, then $x_1(t) \to 0$. If $m_1 f(P^*+\varepsilon) > 1$ then from the above differential inequalities, it follows that
$$\begin{cases} x_1(t) \leq u_1(t), \\ x_2(t) \geq u_2(t). \end{cases}$$
where
$$\begin{cases} u_1' = (\frac{m_1(1-u_1-u_2)}{a_1+(1-u_1-u_2)} f(P^*+\varepsilon) - 1)u_1, \\ u_2' = (\frac{m_2(1-u_1-u_2)}{a_2+(1-u_1-u_2)} - 1)u_2. \end{cases}$$

By Fig. 57, when $\lambda_2 < \lambda^-$, *i. e.* $1 - \lambda_2 > 1 - \lambda^-$, we obtain that $\lim_{t\to\infty} u_1(t) = 0$, $\lim_{t\to\infty} u_2(t) = 1 - \lambda + \varepsilon$, since $x_1(t) \le u_1(t) \to 0$, so $x_1(t) \to 0$ as $t \to \infty$, then $x_2(t) \to 1 - \lambda_2$ and $P(t) \to P^*$ as $t \to \infty$. □

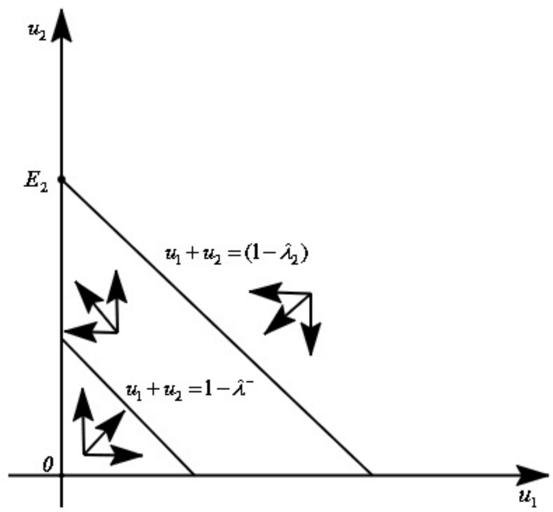

Figure 57:

Theorem 5.6. *If $\lambda_2 < \lambda_1$, then E_1 is GAS.*

Proof. (Exercise!) □

Consider the case $\lambda^- < \lambda_2 < \lambda^+$, then we can show the interior equilibrium $E_c = (x_{1c}, x_{2c}, P_c)$ exists and is unique.

Open problem: If E_c is LAS, then E_c is GAS.
Since the system (3) is a competitive system.

$$\begin{aligned}
x_1' &= (\frac{m_1(1-x_1-x_2)}{a_1+(1-x_1-x_2)} f(P) - 1)x_1, \ \downarrow in\ x_2, \ \downarrow in\ P, \\
x_2' &= (\frac{m_1(1-x_1-x_2)}{a_2+(1-x_1-x_2)} - 1)x_2, \ \downarrow in\ x_1 \\
P' &= (1-P) - \frac{\delta P x_2}{K+P}. \ \downarrow in\ x_2.
\end{aligned}$$

Then Poincare-Bendixson Theorem holds. If E_c is unstable, then exists limit cycle.

Open problem: Prove the uniqueness of limit cycle.

Rock-Scissor-Paper Model of Three Competing Species[CHW]**:**

$$\begin{cases} x_1' = x_1(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3) = f_1(x_1, x_2, x_3), \\ x_2' = x_2(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3) = f_2(x_1, x_2, x_3), \\ x_3' = x_3(1 - \beta_3 x_1 - \alpha_3 x_2 - x_3) = f_2(x_1, x_2, x_3), \\ x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0. \end{cases}$$

(H): $0 < \alpha_i < 1 < \beta_i,\ \alpha_i + \beta_i > 2$.

In above model, species x_1, x_2, x_3 have same intrinsic growth rate $r_1 = r_2 = r_3 = 1$. From assumption (H), we have:

$$\begin{aligned} &x_1 \textit{ outcompetes } x_2 \textit{ as } x_3 = 0, \\ &x_2 \textit{ outcompetes } x_3 \textit{ as } x_1 = 0, \\ &x_3 \textit{ outcompetes } x_1 \textit{ as } x_2 = 0. \ (\textit{See Fig}.58) \end{aligned}$$

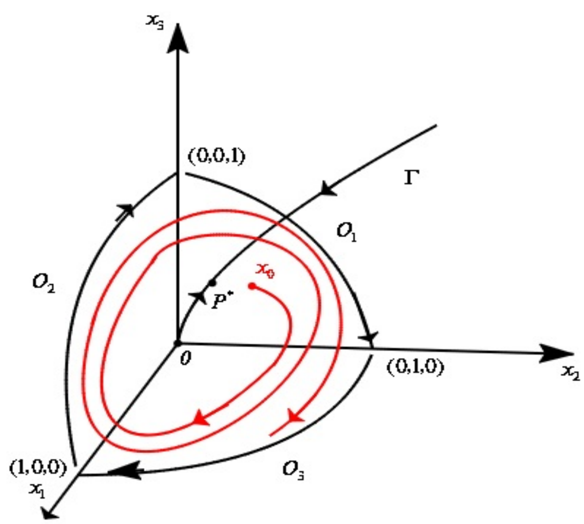

Figure 58:

Case 1: P^* is LAS, then P^* is GAS. (See [CHW])

Case 2: P^* is unstable, then exists one-dim stable manifold Γ, if $x_0 \notin \Gamma$, $w(x_0) = O_1 \bigcup O_2 \bigcup O_3$.(See Fig. 59) (See [CHW])

We prove there is no periodic solution by Stoke's Theorem. Suppose a periodic solution exists with periodic orbit C. Construct vector field $(M_1, M_2, M_3) = (x_1, x_2, x_3) \times (f_1, f_2, f_3)$. Construct a surface S, where the surface S of the cone, formed by joining each point on C to the origin O. $c' = \{(x_1, x_2, x_3) :\ x_1^{\delta_1} x_2^{\delta_2} x_3^{\delta_3} = c\}$. Since $\oint_C M_1 d_{x_1} + \oint_C M_2 d_{x_2} + \oint_C M_3 d_{x_3} = 0$, then based on Stoke's theorem,

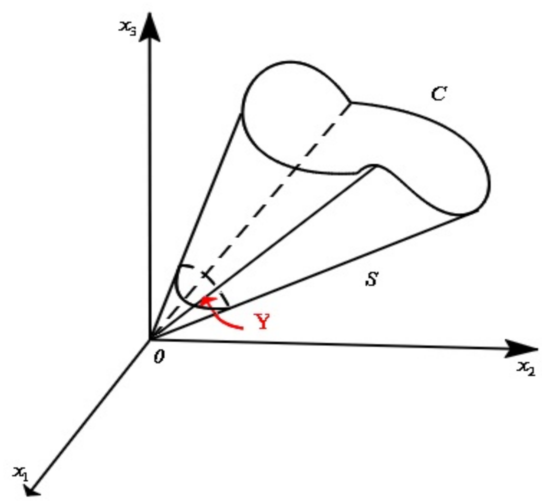

Figure 59:

we obtain $\oint_C M_1 d_{x_1} + \oint_C M_2 d_{x_2} + \oint_C M_3 d_{x_3} = \iint\limits_{YUS} Curl(M_1, M_2, M_3)\vec{n} dA \neq 0$. There is a contradiction.

6 Abstract Theory of Two Species Competition in Ordered Banach Spaces.[HSW]

The ordered Banach Space is denoted by X_i with positive cone X_i^+, s.t. $IntX_i \neq \emptyset$.
Definition: $x_i, \bar{x}_i \in X_i$,

$$x_i \leq \bar{x}_i \Longleftrightarrow \bar{x}_i - x_i \in X_i^+, \bar{x}_i \neq x_i.$$

$$x_i \ll \bar{x}_i \Longleftrightarrow \bar{x}_i - x_i \in IntX_i^+.$$

Let $x_i, y_i \in X_i$, $x_i < y_i$,

$$[x_i, y_i] = \{u \in X_i, x_i \leq u \leq y_i\}.$$

$$[[x_i, y_i]] = \{u \in X_i, x_i \ll u \ll y_i\}.$$

Example: $X_i = \mathbb{R}^n$, $X_i^+ = \mathbb{R}_+^n$, (finite dimensional case)

$$x = (x_1, ..., x_n) \leq y = (y_1, ..., y_n) \Longleftrightarrow x_i \leq y_i, i = 1, 2, ..., n$$

$X_i = C(\Omega, \mathbb{R}^n)$, $X_i^+ = C(\Omega, \mathbb{R}_+^n)$, $\Omega \subseteq \mathbb{R}^n$.(Infinite dimensional case)

$$\varphi \leq \psi \Longleftrightarrow \varphi(x) \leq \psi(x), \forall x \in \Omega.$$

Let

$$X = X_1 \times X_2,\ X^+ = X_1^+ \times X_2^+$$
$$IntX^+ = IntX_1^+ \times IntX_2^+$$
$$K = X_1^+ \times (-X_2^+),$$
$$IntK = IntX_1^+ \times (-IntX_2^+)$$

Then we have

$$x = (x_1, x_2),\ \bar{x} = (\bar{x}_1, \bar{x}_2).$$

(i)ordinary order:

$$x \leq \bar{x} \Longleftrightarrow x_1 \leq \bar{x}_1, x_2 \leq \bar{x}_2.$$

(ii)competitive order:

$$x \leq_K \bar{x} \Longleftrightarrow x_1 \leq \bar{x}_1, \bar{x}_2 \leq x_2.$$

$$x \ll_K \bar{x} \Longleftrightarrow x_1 \ll \bar{x}_1, \bar{x}_2 \ll x_2.$$

Consider two cases

- Monotone map T (discrete)

- Monotone flow T_t (continuous)

Case 1: let $T : X^+ \to X^+$ be continuous and satisfy

(D1) T is order compact and strictly order-preserving $w.r.t <_K$. ie.

$$x <_K \bar{x} \Rightarrow T(x) <_K T(\bar{x}).$$

T is order compact $\Longleftrightarrow$ $T([x_1, 0] \times [0, x_2])$ has compact closure for all $x_1, x_2 > 0$.

(D2) $T(\vec{0}) = \vec{0}$, $\vec{0}$ is a repellering fixed point, ie. $\exists$ bdd U of $\vec{0}$, such that $\forall x \in U$, $\exists n = n(x)$, s.t. $T^n(x) \notin U$.

(D3) $T(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$, $T(\{0\} \times X_2^+) \subset T(\{0\} \times X_2^+)$. s.t. there is a unique $\hat{x}_1 \gg 0$, such that $T(\hat{x}_1, 0) = (\hat{x}_1, 0)$. and there is a unique $\hat{x}_2 \gg 0$ such that $T(0, \hat{x}_2) = (0, \hat{x}_2)$. and $T^n(x_1, 0) \to (\hat{x}_1, 0), \forall x_1 > 0, n \to \infty$. $T^n(0, x_2) \to (0, \hat{x}_2), \forall x_2 > 0, n \to \infty$. (See Fig. 60)

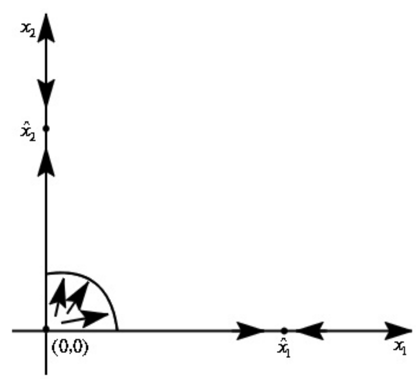

Figure 60:

(D4) If $x, y \in X^+, x <_K y$, and either x or $y \in IntX^+$, then $T(x) \ll_K T(y)$.

Three fixed points $E_0 = (0,0), E_1 = (\hat{x}_1, 0), E_2 = (0, \hat{x}_2)$.

Theorem 6.1. *Let (D1)-(D4) hold, Then $w(x) \subset I$, where $I = [\hat{x}_1, 0] \times [0, \hat{x}_2]$. and exactly one of following three holds*

(a) *There exists a positive fixed point E_* of T in I.*

(b) $T^n(x) \to E_1$ *as* $n \to \infty$. $\forall (x_1, x_2) \in I, x_i \neq 0, i = 1, 2.$

(c) $T^n(x) \to E_2$ *as* $n \to \infty$. $\forall (x_1, x_2) \in I, x_i \neq 0, i = 1, 2.$

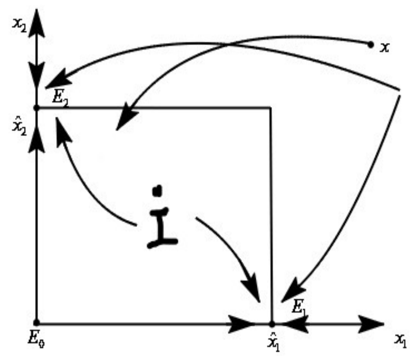

Figure 61:

Finally, if (b) or (c) holds. then $\forall(x_1, x_2) \in X/I, x_i \neq 0, i = 1, 2,$ *such that either* $T^n(x) \to E_1$ *or* $T^n(x) \to E_2$ *as* $n \to \infty$. *(see Fig. 61)*

Example:

$$u_t = d_1 \triangle u + u f_1(t, u, v),$$
$$v_t = d_2 \triangle v + v f_2(t, u, v).$$
$$\frac{\partial f_1}{\partial v} \leq 0, \; \frac{\partial f_2}{\partial u} \leq 0$$
$$f_i(t + w, u, v) = f_i(t, u, v)$$

A monotone map $T : (u(0, \cdot), v(0, \cdot)) \to (u(w, \cdot), v(w, \cdot))$ is a w-periodic map.

Case 2: let $T_t : X^+ \to X^+$ be continuous and satisfy

(C1) T_t is order compact and is strictly order-preserving $w.r.t <_K$. ie.

$$x <_K \bar{x} \Rightarrow T_t(x) <_K T_t(\bar{x}).$$

T_t is order compact $\iff T_t([x_1, 0] \times [0, x_2])$ has compact closure compact, for all $x_1, x_2 > 0$.

(C2) $T_t(\vec{0}) = \vec{0}$, $\vec{0}$ is a repelling equilibrium point, i.e. there exists a neighborhood U of $\vec{0}$, s.t. $\forall x \in U$, $\exists t, \; t = t(x)$, s.t. $T_t(x) \notin U$.

(C3) $T_t(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$, $T_t(\{0\} \times X_2^+) \subset T(\{0\} \times X_2^+)$. s.t. there exists a unique $\hat{x}_1 \gg 0, s.t.\ T_t(\hat{x}_1, 0) = (\hat{x}_1, 0), \forall t > 0$. There exists a unique $\hat{x}_2 \gg 0, s.t.\ T_t(0, \hat{x}_2) = (0, \hat{x}_2), \forall t > 0$. and $T_t(x_1, 0) \to (\hat{x}_1, 0), \forall x_1 > 0, t \to \infty$. $T_t(0, x_2) \to (0, \hat{x}_2), \forall x_2 > 0, t \to \infty$. (see Fig. 62)

(C4) If $x, y \in X^+, x <_K y$, and either x or $y \in IntX^+$, then $T_t(x) \ll_K T_t(y), t > 0$.

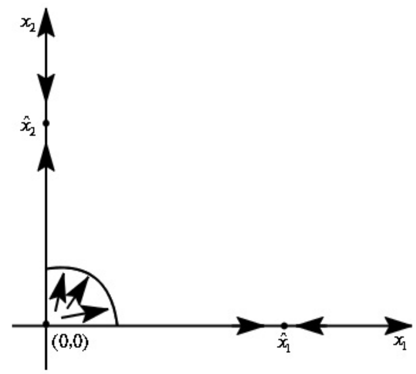

Figure 62:

Three equilibrium points $E_0 = (0,0), E_1 = (\hat{x}_1, 0), E_2 = (0, \hat{x}_2)$.

Theorem 6.2. *Let (C1)-(C4) hold. Then $w(x) \subset I$, where $I = [\hat{x}_1, 0] \times [0, \hat{x}_2]$. and exactly one of following three hold*

(a) $\exists$ *positive equilibrium point E_* of T_t in I.*

(b) $T_t(x) \to E_1$ *as* $t \to \infty$. $\forall (x_1, x_2) \in I, x_i \neq 0, i = 1, 2.$

(c) $T_t(x) \to E_2$ *as* $t \to \infty$. $\forall (x_1, x_2) \in I, x_i \neq 0, i = 1, 2.$

Finally, if (b) or (c) holds. then $\forall (x_1, x_2) \in X/I, x_i \neq 0, i = 1, 2,$ such that either $T_t(x) \to E_1$ or $T_t(x) \to E_2$ as $t \to \infty$.(See Fig. 63)

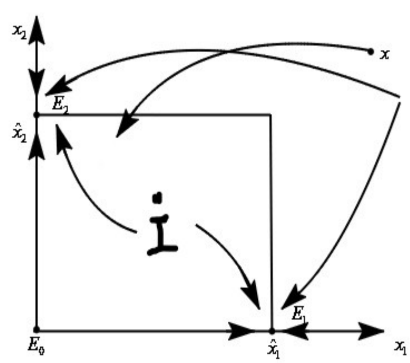

Figure 63:

Example:

$$u_t = d_1 \triangle u + u f_1(u,v),$$
$$v_t = d_2 \triangle v + v f_2(u,v).$$
$$\frac{\partial f_1}{\partial v} \le 0, \frac{\partial f_2}{\partial u} \le 0.$$

We have monotone flow $T_t : (u(0,x), v(0,x)) \to (u(t,x), v(t,x))$.

Dancer-Hess connecting orbits lemma:
Let $u_1 < u_2$ be fixed point of strictly monotone continuous map T.

$$T: \ U \to U, \ I = \ [u_1, u_2]$$

$f(I)$ is precompact. Assume f has no fixed point other than u_1, u_2 in I. Then
(a) $\exists \{x_n\}_{-\infty}^{\infty} \subset I, \ \ x_{n+1} > x_n, \ \ \lim_{n \to -\infty} x_n = u_1, \ \lim_{n \to \infty} x_n = u_2.$
or (b) $\exists \{y_n\}_{-\infty}^{\infty} \subset I, \ \ y_{n+1} < y_n, \ \ \lim_{n \to -\infty} y_n = u_2, \ \lim_{n \to \infty} y_n = u_1$.(See Fig. 64)

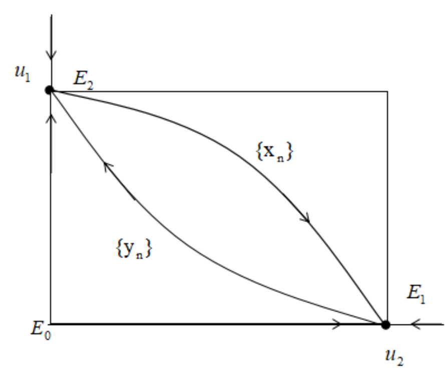

Figure 64:

Dancer-Hess lemma continuous version: Let $u_1 < u_2$ be equilibrium point of strictly monotone continuous semiflow T_t.

$$T_t: \ U \to U, \ I = \ [u_1, u_2]$$

$T_t(I)$ is precompact. Assume T_t has no equilibrium points other than u_1, u_2 in I. Then
(a) $\exists$ *full orbit* $\gamma(t), \gamma(t_1) < \gamma(t_2)$ *as* $t_1 < t_2$. $\gamma(t) \to u_1, \ t \to -\infty, \ \gamma(t) \to u_2$ *as* $t \to +\infty$.
or (b) $\exists \ \gamma(t)$. $\gamma(t_1) < \gamma(t_2)$ *as* $t_1 > t_2, \ \gamma(t) \to u_1, \ t \to +\infty, \ \gamma(t) \to u_2$ *as* $t \to -\infty$.(See Fig. 65)

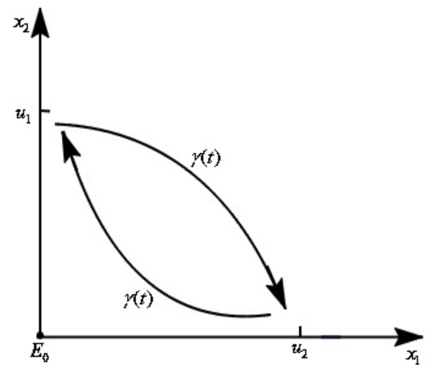

Figure 65:

Next we prove Theorem 1.2. The proof of Theorem 1.1 is similar to the proof of Theorem 1.2. Assume there is no equilibrium in I. Claim (b) (c) cannot hold simultaneously. If not, we choose

$$\gamma_1(t_1) \ near \ E_2,$$

$$\gamma_2(t_2) \ near \ E_1.$$

So

$$\gamma_1(t_1) \ll_K \gamma_2(t_2)$$

we obtain

$$T_t(\gamma_1(t_1)) \ll_K T_t(\gamma_2(t_2))$$

Since $T_t(\gamma_1(t_1)) \to E_1$ as $t \to \infty$,and $T_t(\gamma_2(t_2)) \to E_2$ as $t \to \infty$, we obtain $E_1 \ll_K E_2$, which is a contradiction to $E_2 \leq E_1$.(See Fig. 66)

Next to show:

(a)(b) is incompatible.

(a)(c) is incompatible.

Consider (a) (c) holds

$$\gamma_1(t_1) \ near \ E_1,$$

$$E_* \ll \gamma_1(t_1).$$

we obtain

$$E_* = T_t(E_*) \ll_K T_t(\gamma_1(t_1)), \ \forall \ t > 0.$$

Since $T_t(\gamma_1(t_1)) \to E_2$ as $t \to \infty$, $E_* \ll E_2$, since $E_2 \ll E_* \ll E_1$, hence we obtain a contradiction.(See Fig. 67)

In case that $T_t(x)$ has a positive equilibrium E_* .There are two cases:(see Fig. 68 and Fig.69)

(a) $w(x) = E_*, \ \ \forall \ E_* \leq x \leq E_1.$

(b) $w(x) = E_1, \ \ \forall \ x, \ E_* \leq x \leq E_1.$

by Dancer-Hess Lemma

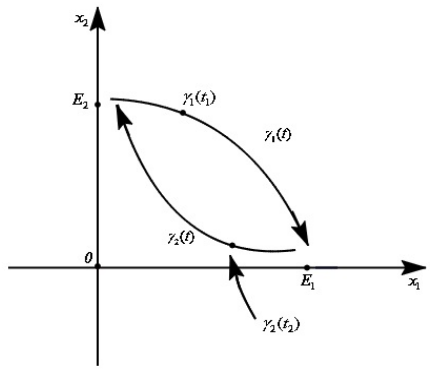

Figure 66:

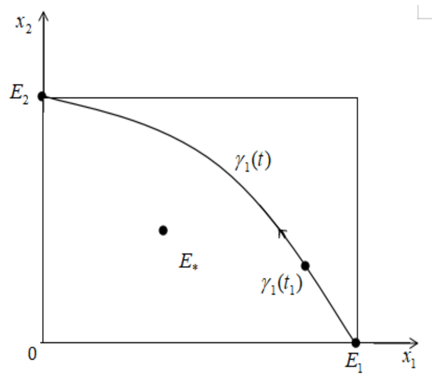

Figure 67:

Theorem 6.3. *If $W^S(E_i) \bigcap Int(X^+) = \emptyset$, where $W^S(E_i)$ is the stable manifold of E_i, then for every $x \in I$, we have $w(x) \in [E^{**}, E_*]$.(See Fig. 70)*

From Theorem 6.2 and 6.3, we have two possibilities:(★)
(i) if there are no positive equilibrium, then $T_t(x) \to E_1$ or $T_t(x) \to E_2$.
(ii) if the positive equilibrium is unique, then $T_t(x) \to E^*$.

These are elliptic problems.
Example: Two species competes for light in a water column.(See Fig. 71)

$$(1.1)\begin{cases} u_t = D_1 u_{xx} - \alpha_1 u_x + (g_1(I(x,t)) - d_1)u_1, \\ v_t = D_2 v_{xx} - \alpha_2 v_x + (g_2(I(x,t)) - d_2)u_2. \end{cases}$$

$$(1.2)\ I(x,t) = I_0 exp[-k_0 x - \int_0^x (k_1 u(s,t) + k_2 v(s,t) ds]$$

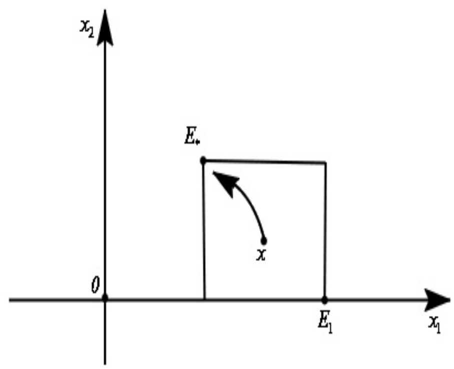

Figure 68:

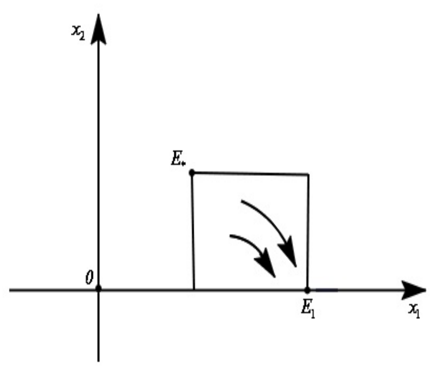

Figure 69:

Boundary conditions (No flux at x=0 and x=L)

$$(1.3)\begin{cases} D_1 u_x(x,t) - \alpha_1 u(x,t) = 0 \;\; at\ x = 0, L.\ t > 0, \\ D_2 v_x(x,t) - \alpha_2 v(x,t) = 0 \;\; at\ x = 0, L.\ t > 0. \end{cases}$$

$$I.C. \;\; (1.4) \quad u(x,0) = u_0(x) \quad v(x,0) = v_0(x), \; 0 < x < L$$

Du and Hsu[DH] prove the case of single population growth under the assumption $0 < d_1 < d_1^*$ (some kind of principal eigenvalue)

As $v \equiv 0$, $u(x,t) \to \hat{u}(x)$. $\hat{u}(x)$ is the unique steady state.(See Fig. 72). Jiang Lou, Lam and Wang ([JLLW]). prove Theorem 6.4 under special cone

$$K = K_1 \times (-K_1)$$

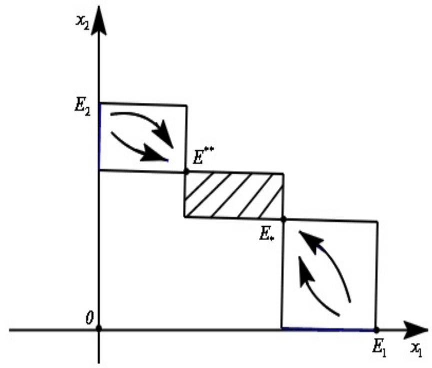

Figure 70:

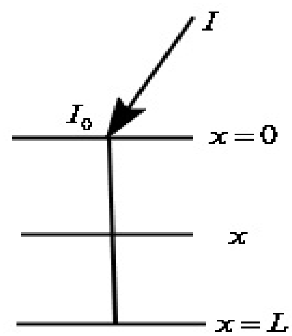

Figure 71:

$$K_1 = \{\phi \in C([0, L], R) : \int_0^x \phi(s)ds \geq 0,\ x \in [0, L]\}$$

$$IntK_1 = \{\phi \in C([0, L], R) : \phi(0) > 0,\ \int_0^x \phi(s)ds > 0,\ x \in [0, L]\}$$

$$IntK = IntK_1 \times (-IntK_1)$$

Theorem 6.4. *The system (1.1)-(1.4) is a strongly monotone dynamical system. w.r.t.*$\leq_K$*, i.e. if* $(u_1(\cdot, 0), v_1(\cdot, 0)) \leq_K u_2(\cdot, 0), v_2(\cdot, 0))$ *then* $(u_1(\cdot, t), v_1(\cdot, t)) \leq_K u_2(\cdot, t), v_2(\cdot, t))\ \ \forall\ t > 0$.

Open problem: To find conditions such that (★) holds.

Unstired chemostat[HW1]:

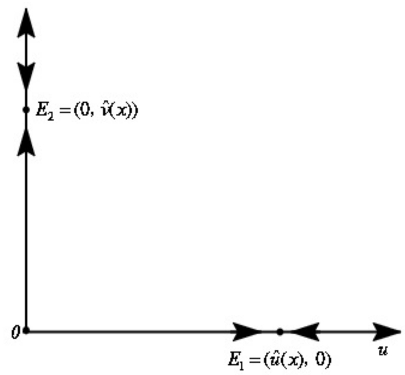

Figure 72:

$$PDE \begin{cases} S_t = dS_{xx} - uf_1(S) - vf_2(S), \\ u_t = du_{xx} + uf_1(S), \\ v_t = dv_{xx} + vf_2(S). \end{cases} \tag{1}$$

$$B.\ C.\quad S_x(t,0) = -S^{(0)} \qquad S_x(t,1) + rS(t,1) = 0$$

$$u_x(t,0) = 0 \qquad u_x(t,1) + ru(t,1) = 0$$

$$v_x(t,0) = 0 \qquad v_x(t,1) + rv(t,1) = 0$$

$$I.\ C.\ u(0,x) = u_0(x),\ v(0,x) = v_0(x),\ S(0,x) = S_0(x).$$

Step 1: Prove conservation law.

$$S(t,x) + u(t,x) + v(t,x) \to \phi(x)\ as\ t \to \infty\ uniform\ in\ x,$$

$$\phi(x) = S^{(0)}(\frac{1+r}{r} - x).$$

Step 2: Consider limiting system.

$$PDE \begin{cases} u_t = du_{xx} + uf_1(\phi(x) - u - v), \\ v_t = dv_{xx} + vf_2(\phi(x) - u - v). \end{cases} \tag{2}$$

and verify if $(u,v) \leq_K (\bar{u},\bar{v})$, then $T_t(u,v) \leq_K T_t(\bar{u},\bar{v})$ for $t > 0, i.e.$ it is strongly monotone dynamical system, where

$$(u,v) \leq_K (\bar{u},\bar{v}) \Leftrightarrow u(x) \leq \bar{u}(x),\ \bar{v}(x) \leq v(x),\quad \forall\ x \in [0,1]$$

We note that system (1) and system (2) have the same solution behavior by [Z1](P. 17).

Step 3: Prove global behavior of $u(x,t)$ as $v(x,t) \equiv 0$,($v(x,t)$ as $u(x,t) \equiv 0$)

$$|u(x,t) - \hat{u}(x)| \to 0 \ as \ t \to \infty, \ (|v(x,t) - \hat{v}(x)| \to 0 \ as \ t \to \infty)$$

where $\hat{u}(x)$ is the unique steady state (where $\hat{v}(x)$ is the unique steady state).

Step 4: Stability analysis of $(\hat{u}, 0)$ and $(0, \hat{v})$.

Linearization and principal eigenvalue.

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